

AN ABSTRACT OF THE THESIS OF

Paul T. Bellatty for the degree of Doctor of Philosophy in Animal Science presented on April 30, 1987.

Title: Genetic Components of Genetic Influence on Traits of Purebred and Crossbred Populations of Swine of Berkshire and Yorkshire Origin

Abstract approved

*Redacted for Privacy*

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Purebred and crossbred litters of Yorkshire and Berkshire breeds of swine were evaluated for number of piglets born alive per litter, number of piglets weaned per litter, mean piglet birth weight, mean piglet birth weight adjusted for number of piglets born alive per litter and mean piglet weaning weight. The 632 litters, adjusted to a sow equivalent, were weaned at 56 days. The data were subjected to two analyses; the first calculates paternal, maternal and litter heterosis as the difference between crossbred and purebred means. The second analysis calculates estimates using an additive-dominance model and an epistatic model; model and scale are tested for appropriateness.

In the first analysis, litter heterosis estimates tend to be positive, to range between 5% and 11%, and are similar to estimates in the literature. Maternal heterosis estimates are positive for number born and weaned, zero for birth weight and negative for

weaning weight. Except weaning weight, these are similar to estimates in the literature. Paternal heterosis estimates are negative for number born and weaning weight and positive for number weaned and birth weight.

In the second analysis, which uses both nontransformed and log base 10 transformed data, the additive-dominance model is not appropriate for any trait with nontransformed or transformed scales; estimates are similar to these of the first analysis. The appropriate model is the epistatic model for all traits; the nontransformed scale is appropriate for birth weight adjusted for number born and the transformed scale is appropriate for number born, number weaned, weaning weight and birth weight adjusted for number born. Parameter estimates attaining statistical significance for number born are the mean, maternal additive, paternal dominance, litter dominance, and the litter additive X additive epistatic interaction. For number weaned, significant parameter estimates are the mean, maternal additive, paternal dominance, litter dominance, and litter additive X additive. For birth weight unadjusted for number born, significant estimates are the mean, maternal additive, paternal dominance, and maternal additive X additive; no parameters are significant for birth weight adjusted for number born. Significant estimates for weaning weight are mean, litter additive, maternal dominance, and maternal dominance X dominance. Differences between estimates for the first analysis and the second analysis are large for some estimates of heterosis.

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Genetic Components of Genetic Influence on Traits  
of Purebred and Crossbred Populations of Swine  
of Berkshire and Yorkshire Origin

by

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# GENETIC COMPONENTS OF GENETIC INFLUENCE ON TRAITS OF PUREBRED AND CROSSBRED POPULATIONS OF SWINE OF BERKSHIRE AND YORKSHIRE ORIGIN

## INTRODUCTION

Genetic parameters are generally calculated with the assumption that both epistatic interactions and scale effects are negligible within a population. Breeding plans are established based upon these estimates and recommendations are made to maximize genetic progress and productivity. This situation exists due to the large volume and type of data required to accurately estimate epistatic and scale effects.

A unique experiment was conducted at the Oregon State University Swine Unit to examine Yorkshire and Berkshire breed and heterosis effects for purebred and crossbred breed types. These genetically diverse breeds of swine provide an excellent opportunity to calculate genetic parameters i) assuming no epistatic interactions or scale effects and ii) without assuming the absence of epistatic and scale effects.

Chapter 1 examines breed effects, maternal heterosis, paternal heterosis and individual heterosis for reproductive characters of Yorkshire and Berkshire purebreds and crossbreds. Calculations of parameter estimates assume no epistatic interactions and are presented in the scale commonly found in the literature. Chapter 2 presents the same genetic parameters using epistatic models and

appropriate scales; no estimates of epistasis for reproductive characters in swine are available. Chapter 2 also explains epistatic coefficients in terms of genetic configurations based upon genetic expectations of the sire, dam and litter. This method gives meaning to the epistatic coefficients and simplifies interpretation.

HETEROSIS CALCULATED AS THE DIFFERENCE BETWEEN  
PUREBRED AND CROSSBRED MEANS

ABSTRACT

Purebred and crossbred Yorkshire and Berkshire litters were evaluated for number born alive and weaned per litter and for mean piglet birth and 56-day weaning weights. A Composite breed, originated from an F2 X F2 cross, is assumed to possess similar proportions of Yorkshire and Berkshire genes. The data were adjusted to a sow equivalent and analyzed on an expected proportion of Yorkshire-Berkshire genetic basis.

Purebred sow means exceed gilt means for numbers born and weaned per litter and mean piglet birth weight; gilt means exceed sow means for mean piglet weaning weight. Parity differences for numbers born alive and weaned per litter and mean piglet weaning weight are largest for the Berkshires and intermediate for the Composites. Parity differences are small for mean piglet birth weight.

Among the purebreds, Berkshire means are smallest for numbers born and weaned per litter and largest for piglet weights. Composite means exceed Yorkshire means for all traits except mean piglet weaning weight.

Individual heterosis estimates are 8% and 11% for numbers born and weaned per litter, respectively. Individual heterosis for mean piglet weight at birth, weaning, and at birth after adjustment for

litter size range from 5% to 7%. Maternal heterosis estimates are 11%, 22% -4%, -16% and 0% for number born alive per litter, number weaned per litter, mean piglet birth weight, mean piglet weaning weight, and mean piglet birth weight adjusted for litter size, respectively. The paternal heterosis estimate for number born alive is -10%, for number weaned per litter is 6%, for mean piglet birth weight is 13%, for mean piglet weaning weight is -15% and for mean piglet birth weight adjusted for litter size is 9%. Estimates of breed means, maternal heterosis and litter heterosis are generally similar to those in the literature.

## INTRODUCTION

The swine industry desires to utilize genetic and environmental influences to maximize efficiency of production. Genetic contributors include the use of artificial selection, breed complementation, inbreeding, development of new breeds or lines, use of exotic breeds, and heterosis. Hybrid vigor or heterosis is the result of combining genetically diverse lines or breeds to maximize heterozygosity in the sire, dam or litter. England and Winters (1953) report crosses to be less variable than parental lines, and to exhibit more heterosis for preweaning traits than for postweaning traits. O'Ferrall et al. (1968) report that crossbred litters are significantly larger and heavier at 21 and 56 days of age. More recently, Young et al. (1976) and Johnson et al. (1978) report significant increases in litter size at weaning due to heterosis.

Generally the lowly heritable traits are affected less by selection and decline more in production when inbreeding is used; however, they respond favorably to crossbreeding. Accurate estimates of heterosis are required to establish the most productive breeding systems. Our study uses a popular breed selected for its reproductive characteristics, the Yorkshire breed, and a less popular breed selected for its carcass characteristics, the Berkshire breed. This study evaluates the reproductive performance of purebred and crossbred litters and estimates paternal, maternal and litter heterosis in crosses involving these diverse breeds of swine.

## MATERIALS AND METHODS

Six-hundred-thirty-two gilts and sows that farrowed litters between 1967 and 1975 were evaluated for number of piglets born alive and weaned per litter, mean piglet weight at birth and at weaning. Data has been adjusted to a sow equivalent before the analyses were conducted.

The pigs were raised in complete confinement at the Oregon State University Swine Unit in a Specific-Pathogen-Free type environment. Gilts were selected as broodstock animals at 6 months of age, stimulated to cycle by mixing with unfamiliar gilts in the vicinity of boars and exposed to boars at third estrus. Gilts that conceived were transferred to farrowing crates at 110 days. Piglets were weaned at 56 days postfarrowing when dams were moved to the broodstock barn; dams were rebred on first estrus.

Yorkshire (Y), Berkshire (B) and Composite (C) breeds were mated in various combinations to create three purebred and 12 crossbred breeding types. The Composite breed, originated from reciprocal Yorkshire X Berkshire crosses, is the F3, F4 and subsequent generations; by intentional design, the Composite had the opportunity to possess equal proportions of Berkshire and Yorkshire genes and is assumed to do so.

Individual, maternal and paternal heterosis estimates are calculated on a percentage of Yorkshire-Berkshire genes basis. Individual heterosis is calculated as the difference between the average of reciprocal Yorkshire X Berkshire and Berkshire X

Yorkshire (sire X dam) means and the average of the purebred parental means. To express individual heterosis as a percent, the deviation between crossbred and parental means is divided by the average of parental least-squares means and multiplied by 100. Maternal heterosis calculations by breed of dam are listed below; numerators represent deviations between crossbred and parental means and denominators are used to express heterosis as a percent.

<u>Dam</u>	<u>Equation</u>
F1	$[\bar{X}_{cb} - 1/2(\bar{X}_b + \bar{X}_y) - 1/2H^i] / [1/2(\bar{X}_b + \bar{X}_y)]$
Composite	$2[\bar{X}_{cb} - 1/2(\bar{X}_b + \bar{X}_y) - 1/2H^i] / [1/2(\bar{X}_b + \bar{X}_y)]$

where

$\bar{X}_{cb}$	is the crossbred mean
$\bar{X}_b$	is the purebred Berkshire mean
$\bar{X}_y$	is the purebred Yorkshire mean
$H^i$	is individual heterosis

Similar to accounting for maternal effects by taking the mean of reciprocal crosses for individual heterosis estimates, the least-squares means of Berkshire and Yorkshire sires for each dam breed accounts for sire and litter breed effects when calculating maternal heterosis. A third pair of breed means are averaged for another estimation of maternal heterosis. The breeds and equations

used to calculate the third estimate of maternal heterosis is presented below.

<u>Breed</u>	<u>Equation</u>
B{C X Y}	$2[\bar{X}_{cb} - 3/4\bar{X}_y - 1/4\bar{X}_b - 3/4H^i] / [3/4\bar{X}_y + 1/4\bar{X}_b]$
Y{C X B}	$2[\bar{X}_{cb} - 1/4\bar{X}_y - 3/4\bar{X}_b - 3/4H^i] / [1/4\bar{X}_y + 3/4\bar{X}_b]$

Doubling the numerator for Composite, C X Y, and C X B dams adjusts the estimate to the F1 or a 100% level of heterozygosity. The paternal heterosis estimate for Composite sires mated to Yorkshire and Berkshire dams is calculated with the following formula:

$$2[\bar{X}_{cb} - 1/2(\bar{X}_b + \bar{X}_y) - 1/2H^i] / [1/2(\bar{X}_b + \bar{X}_y)]$$

The least-squares means from C X B and C X Y breeds are used in the formula above to estimate paternal heterosis. Maternal and breed effects are accounted for by averaging paternal heterosis estimates from each breed.

## RESULTS

Purebred differences between gilt and sow means are in table 1.1. Sow means are larger than gilt means for numbers born alive and weaned per litter. Sow and gilt differences for mean piglet birth weight are about .10 kg for Berkshire and Composite breeds and zero for the Yorkshire breed. Mean parity differences for piglet weaning weight range from -0.49 kg for the Yorkshires to -2.88 kg for the Berkshires. For numbers born alive and weaned per litter, differences are largest for the Berkshires, intermediate for Composite and smallest for Yorkshires. The same relative ranking holds for mean piglet weaning weight except the signs of the differences are negative.

Means adjusted to a sow equivalent and standard errors calculated from combining gilt and sow variances for nontransformed and transformed data are in table 1.2 and 1.3, respectively. Breed means, where breed refers to the litter's breed type, for Berkshire dams are the lowest of those breeds examined for number of piglets at birth and weaning. Yorkshire and Composite dam means range from 9.93 to 11.17 piglets at birth; F1 dam means range from 9.76 to 11.75 with the C X F1 breed being the most prolific at birth for all breeds examined. A 3% difference exists between breed means for Yorkshire and Berkshire sires when mated to Composite dams for number of piglets born alive per litter. The mean difference between numbers born alive per litter for Berkshire and Yorkshire sires mated to F1 dams is 11% and the B{C X Y} and the Y{C X B}

TABLE 1.1 PUREBRED ADJUSTMENTS FROM A GILT TO A SOW EQUIVALENT

<u>Trait</u>	<u>Berkshire</u>	<u>Yorkshire</u>	<u>Composite</u>
Number piglets born alive per litter	2.15	0.47	1.16
Number piglets weaned per litter	1.67	0.20	1.00
Mean piglet birth weight (kg)	0.10	0.00	0.11
Mean piglet weaning weight (kg)	-2.88	-0.49	-1.06

TABLE 1.2. NUMBERS TESTED (N), MEANS AND STANDARD ERRORS (SE) WITH THE NONTRANSFORMED SCALE

Breed	N <sup>1</sup>	Number born per litter		Number Weaned per litter		Piglet birth wt.-unadjusted (kg)		Piglet weaning wt. (kg)		Piglet birth wt.-adjusted (kg)
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean
Berkshire (B)	8/40	7.90	.40	6.55	.35	1.429	.036	16.57	0.99	1.333
Yorkshire (Y)	35/80	10.70	.28	8.14	.26	1.210	.023	13.45	0.46	1.233
Composite (C)	20/41	10.71	.21	8.90	.24	1.292	.019	12.80	0.31	1.315
B X Y	7/12	10.58	.73	8.42	.76	1.275	.031	15.43	1.01	1.293
Y X B	1/16	9.44	.40	7.94	.39	1.495	.123	16.20	0.45	1.464
B X C	13/4	10.25	.50	9.25	.59	1.279	.041	15.61	0.66	1.326
C X B	11/5	7.20	.44	7.00	.32	1.501	.083	15.29	1.04	1.375
Y X C	9/14	9.93	.50	8.79	.54	1.264	.043	14.36	1.13	1.254
C X Y	14/6	11.17	.49	9.00	.46	1.356	.048	13.30	0.73	1.399
B X F1	6/15	9.87	.73	8.47	.62	1.347	.049	13.34	0.85	1.335
B{C X Y}	16/34	11.50	.46	9.32	.46	1.303	.046	12.73	0.47	1.360
Y X F1	17/29	11.10	.33	9.03	.35	1.400	.034	14.28	0.67	1.440
Y{B X C}	28/67	9.55	.28	7.95	.29	1.390	.022	13.60	0.51	1.364
C X F1	14/24	11.75	.39	10.38	.38	1.361	.029	15.37	0.77	1.429
F2	13/33	9.76	.50	8.27	.40	1.471	.046	13.01	0.55	1.454

<sup>1</sup> Numbers for gilts/sows

TABLE 1.3. NUMBERS TESTED (N), MEANS AND STANDARD ERRORS (SE) WITH THE TRANSFORMED SCALE

Breed	N <sup>1</sup>	Number born per litter		Number Weaned per litter		Piglet birth wt.-unadjusted (kg)		Piglet weaning wt. (kg)		Piglet birth wt.-adjusted (kg)
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean
Berkshire (B)	8/40	0.862	.027	.778	.028	.150	.011	1.191	.022	.115
Yorkshire (Y)	35/80	1.002	.015	.873	.018	.072	.009	1.097	.015	.077
Composite (C)	20/41	1.020	.013	.934	.019	.106	.009	1.093	.015	.116
B X Y	7/12	1.001	.039	.895	.050	.103	.011	1.176	.031	.108
Y X B	1/16	0.956	.035	.877	.037	.169	.019	1.199	.026	.161
B X C	13/4	0.980	.029	.956	.047	.104	.014	1.188	.020	.123
C X B	11/5	0.857	.024	.845	.020	.173	.023	1.171	.034	.137
Y X C	9/14	0.984	.024	.924	.032	.097	.015	1.125	.033	.097
C X Y	14/6	1.042	.024	.943	.025	.129	.017	1.106	.023	.145
B X F1	6/15	0.956	.040	.892	.041	.154	.027	1.147	.044	.146
B{C X Y}	16/34	1.042	.022	.933	.033	.109	.011	1.091	.016	.125
Y X F1	17/29	1.033	.016	.931	.022	.141	.014	1.139	.019	.155
Y{B X C}	28/67	0.956	.027	.875	.021	.137	.007	1.095	.018	.129
C X F1	14/24	1.060	.018	1.002	.018	.130	.009	1.165	.020	.151
F2	13/33	0.958	.029	.891	.026	.163	.012	1.099	.019	.155

<sup>1</sup> Numbers for gilts/sows

breed means differ by 17%. Relative to the Yorkshire sire, the Berkshire sire is associated with smaller litters at birth when mated to Composite and F1 dams, yet prolificacy of the Y{C X B} is only 83% the level of the B{C X Y} breed mean. Composite sires are associated with the large litter means at birth when mated to Yorkshire or F1 dams, but are the least prolific of all the breeds examined when mated to Berkshire dams. Sire differences may reflect maternal ability of the dam and may not be influenced by the sire breed.

For number of piglets weaned per litter, the C X F1 breed mean is more than one piglet greater than any other breed mean evaluated. As with mean number of piglets born alive per litter, the Berkshire dams have the fewest mean number of piglets weaned per litter. Berkshire sires mated to Composite and C X Y dams are associated with the second and third largest means for number weaned per litter, respectively. Thus the Berkshire dams tend to produce fewer piglets per litter at birth and weaning while the Berkshire sires tend to produce larger litters if mated to Composite or Composite crosses of dam. Purebred Yorkshire dam means for numbers at weaning are smallest when mated to Yorkshire sires, intermediate when mated to Berkshire sires and largest when mated to Composite sires; for number born alive per litter, the ranking of sires is different. Composite dams tend to produce the least number at weaning when mated to Yorkshire sires, intermediate with Composite sires, and the largest litters when mated to Berkshire sires. Litter means from F1 dams are 8.47 piglets at

weaning when mated to Berkshire sires, 9.03 when mated to Yorkshire sires and 10.38 when mated to Composite sires.

The correlation between mean number of piglets born alive per litter and mean unadjusted piglet birth weight is  $-.58$ . The C X B breed, which is associated with the smallest number of piglets per litter at birth, is associated with the largest mean piglet birth weight. The Y X B and F1 X F1 breeds have large breed means for mean piglet birth weight. The purebred Yorkshire mean is the lowest at 1.21 kg followed by the Y X C, B X Y, and the B X C breed means. Berkshire and F1 dams tend to have litters with heavy piglets and both Yorkshire and Composite dams tend to have piglets which are lighter at birth.

The correlation between the means of mean unadjusted piglet birth and piglet weaning weight is  $.32$ . The purebred Berkshire, the Y X B, the B X C and the C X F1 breeds have the largest mean piglet weaning weights. The C X F1 breed mean for number born alive and weaned per litter are the largest of the breeds evaluated. The Composite, B{C X Y} and the F2 means are the lowest for mean piglet weaning weight for the breeds evaluated. The B X C breed, associated with a relatively low mean piglet birth weight, has the third heaviest mean for mean piglet weaning weight. Interestingly, F2 X F2 and F1 X F1 cross means for piglet weaning weight are low while the C X F1 cross mean is high. Sires, dams and litters are assumed to contain similar amounts of Berkshire and Yorkshire genes for all three types of breeding. Means for mean piglet birth weight adjusted for litter size are similar to the unadjusted means. The purebred Yorkshire and the Y X C means are

lowest of the breeds examined for adjusted mean piglet weaning weight while the Y X B and F1 X F1 breeds are associated with the largest means.

Individual heterosis estimates for nontransformed and log base 10 transformed data are in table 1.4. Crossbred litters from purebred Berkshire and Yorkshire dams average .71 and .84 more piglets born and weaned per litter, respectively. Mean piglet birth weights average about .08 to .10 kg more for the crossbreds relative to the Berkshire and Yorkshire purebreds. The average superiority of the B X Y and Y X B crossbred piglets at weaning relative to their Berkshire and Yorkshire contemporaries is .81 kg. The increase in production attributed to the hybrid vigor of the piglets is between 5% and 11% for all traits examined. The same estimates of individual heterosis calculated using the log base 10 scale are 5% for number born alive per litter, 7% for numbers weaned per litter, 23% for mean piglet birth weight unadjusted for litter size, 40% for birth weight adjusted for litter size and 4% for mean piglet weaning weight.

Maternal heterosis estimates calculated from three pairs of least-squares means are presented as deviations and percentages in tables 1.5 and 1.6, respectively; the three pairs of breeds are B X F1 and Y X F1, B X C and Y X C, and B{Y X C} and Y{B X C}. Least-squares estimates for all breeds are positive for number born alive and weaned per litter, and tend to be negative for unadjusted mean piglet birth weight and mean piglet weaning weight. For numbers born alive per litter, F1 and Composite dams average about .85 more piglets at birth relative to the purebred Berkshires

TABLE 1.4 ESTIMATES OF INDIVIDUAL HETEROSIS FROM RECIPROCAL  
CROSSES OF BERKSHIRE AND YORKSHIRE LITTERS FROM PUREBRED DAMS

Trait -----	Nontransformed		Transformed (log 10)	
	Deviation	Percent	Deviation	Percent
-----	-----	-----	-----	-----
Number born alive per litter	0.71	7.63	.047	4.99
Number weaned per litter	0.84	11.37	.061	7.33
Mean piglet birth weight (kg) (unadjusted)	0.08	6.21	.025	22.52
Mean piglet weaning weight (kg)	0.81	5.36	.044	3.80
Mean piglet birth weight (kg) (adjusted)	0.10	7.44	.039	40.10

TABLE 1.5. MATERNAL HETEROSIS ESTIMATES EXPRESSED AS DEVIATIONS FROM THE BERKSHIRE AND YORKSHIRE PUREBRED MEANS FOR NONTRANSFORMED (NT) AND TRANSFORMED (N) DATA

Trait	Breed of dam <sup>1</sup>							
	Y X B		Composite		Y X C and B X C		Mean	
	NT	T	NT	T	NT	T	NT	T
Number born alive per litter	0.830	0.039	0.870	0.053	1.385	0.063	1.028	0.052
Number weaned per litter	0.985	0.056	2.510	0.168	1.320	0.066	1.605	0.097
Mean piglet birth weight (kg) (unadjusted)	0.029	0.024	-0.146	-0.046	-0.037	-0.014	-0.051	0.012
Mean piglet weaning weight (kg)	-1.603	-0.023	-0.885	-0.019	-4.898	-0.167	-2.462	-0.070
Mean piglet birth weight (kg) (adjusted)	0.057	0.035	-0.082	-0.011	0.029	0.004	0.001	0.010

<sup>1</sup> breed of litter and sire are accounted for by taking least-squares means of Berkshire and Yorkshire sires

TABLE 1.6. MATERNAL HETEROSIS ESTIMATES EXPRESSED AS PERCENTS FROM THE BERKSHIRE AND YORKSHIRE PUREBRED MEANS FOR NONTRANSFORMED (NT) AND TRANSFORMED (N) DATA

Trait	Breed of dam <sup>1</sup>							
	Y X B		Composite		Y X C and B X C		Mean	
	NT	T	NT	T	NT	T	NT	T
-----	-----	---	-----	---	-----	---	-----	---
Number born alive per litter	8.93	4.19	9.36	5.69	15.99	7.05	11.43	5.64
Number weaned per litter	13.41	6.75	34.18	20.40	18.64	8.16	22.08	11.77
Mean piglet birth weight (kg) (unadjusted)	2.23	21.63	-11.20	-41.45	-2.62	-8.56	-3.86	-9.46
Mean piglet weaning weight (kg)	-10.68	-1.99	-5.70	-1.63	-32.37	-14.60	-16.25	-6.07
Mean piglet birth weight (kg) (adjusted)	4.42	36.67	-6.36	-11.05	1.18	5.09	-0.25	10.24

<sup>1</sup> breed of litter and sire are accounted for by taking least-squares means of Berkshire and Yorkshire sires

and Yorkshires. The mean increase in number born alive per litter attributed to the crossbred dam for Y X C and B X C dams is 1.39 piglets; the least-squares mean for maternal heterosis is 1.03 piglets per litter averaged across breed of dam. These deviations expressed as percentages are 9% for F1 and Composite dams, 16% for the Y X C and B X C dams and 11% averaged across breed of dam. Thus a Berkshire X Yorkshire dam is expected to average one more piglet at birth representing an 11% increase in the number of piglets born alive per litter. F2 dams, with 1/2 the expected heterozygosity as the F1 dams, would be expected to increase the numbers born per litter by 1/2 the amount of the F1 dams. Maternal heterosis estimates for number of piglets weaned per litter are similar to those for numbers born alive for the F1 and Y X C or B X C dams. However, estimates for numbers weaned are three times those for numbers born alive per litter for the Composite breed of dam. The difference between the Composite dam estimates for number born alive and weaned per litter translates into an average maternal heterosis estimate of 1.61 piglets per litter or a 22% increase in numbers weaned per litter. Thus, on the average dams containing maximum heterozygosity are expected to wean 1.6 more piglets per litter and increase numbers at weaning by 22% over the purebred Berkshire and Yorkshire dams.

The crossbred dam is expected to produce piglets weighing less at birth than the mean of the Berkshires and Yorkshires. Although the F1 dams average piglets weighing .03 kg more at birth relative to the Berkshire and Yorkshire purebreds, the Composite dams and the average of the Y X C and B X C tend to have piglets which weigh

less; the least-squares maternal heterosis estimate for mean piglet birth weight is  $-.05$  kg. This decrease of  $.05$  reflects a decrease in mean piglet birth weight of 4% attributable to the crossbred dam. This result may reflect the larger number of piglets born per litter. The least-squares mean for piglet birth weight adjusting for litter size approximates zero. A larger decrease in piglet weight is apparent in evaluating weaning weight. Estimates for the influence of maximum heterozygosity between Berkshire and Yorkshire breeds in the dam range from  $-.89$  kg to  $-4.90$  kg and average  $-2.46$  kg per piglet. On the average, crossbred dams produce piglets weighing 16% less at weaning relative to litters from Berkshire and Yorkshire dams. Least-squares means for maternal heterosis estimates with the transformed scale are 6% for numbers born alive per litter, 12% for number weaned per litter,  $-9\%$  for mean piglet birth weight unadjusted for litter size, 10% for mean piglet birth weight adjusted for litter size, and  $-6\%$  for mean piglet weaning weight. The relative contributions of dam breed to each least-squares mean for maternal heterosis is similar with both scales.

Paternal heterosis estimates are calculated with C X Y and C X X B least-squares means. On the average, a 100% crossbred sire from a B X Y mating is expected to produce  $.9$  fewer piglets at birth,  $.5$  more piglets at weaning with piglets weighing  $.17$  kg more at birth and  $2.24$  kg less at weaning (table 1.7). Adjusting for litter size, the crossbred boar is expected to increase the mean piglet birth weight by  $.11$  kg. Paternal heterosis estimates, expressed as a percentage for nontransformed and transformed

TABLE 1.7 ESTIMATES OF PATERNAL HETEROISIS FROM COMPOSITE X YORKSHIRE  
AND COMPOSITE X BERKSHIRE BREEDS

Trait -----	Nontransformed		Transformed (log 10)	
	Deviation	Percent	Deviation	Percent
	-----			
Number born alive per litter	-0.94	-10.11	-.012	-1.29
Number weaned per litter	0.47	6.40	.076	9.26
Mean piglet birth weight (kg) (unadjusted)	0.17	12.88	.055	49.55
Mean piglet weaning weight (kg)	-2.24	-14.89	-.055	-4.77
Mean piglet birth weight (kg) (adjusted)	0.11	8.76	.051	53.55

scales, respectively, are -10% and -1% for numbers born alive per litter, 6% and 9% for number weaned per litter, 13% and 50% for mean piglet birth weight unadjusted for litter size, 9% and 54% for mean piglet birth weight adjusted for litter size, and -15% and -5% for mean piglet weaning weight.

## DISCUSSION

Average parity differences for Berkshire, Yorkshire and Composite breeds are larger than literature estimates for number of piglets born per litter. The Berkshire breed is associated with the largest parity difference and is a breed generally not included in cited studies. Reported purebred parity differences range from .08 (Fahmy et al., 1971) to .67 (Johnson et al., 1978) relative to 1.26 for this study. Purebred parity differences of .96 piglets per litter at weaning reported here are similar to estimates in the literature of .32 (Fahmy et al., 1971) .60 at 21 days postfarrowing (Holtmann et al., 1975) and 1.62 (Johnson et al., 1978).

Differences between literature estimates and those obtained in this study are small; the Berkshire breed however, does tend to increase purebred parity differences for numbers born and weaned per litter.

Mean parity differences are .07 kg and -1.48 kg for Berkshire, Yorkshire and Composite breeds for mean piglet birth and weaning weights, respectively. Average gilt and sow differences are .13 kg (Johnson et al., 1978) .09 kg (Holtmann et al., 1975) and .10 kg (Fahmy et al., 1971) for mean piglet birth weight. Differences between parities for mean piglet weaning weight have been reported: Johnson et al. (1978), 1.25 kg; Fahmy et al. (1971), .51 kg; and Holtmann et al. (1975), .51 kg for weights measured at 21 days. Although the Berkshire breed is associated with the largest differences between parity means for mean piglet weaning weight, purebred gilts in this study had heavier mean piglet weights at

weaning than did the purebred sows. Differences between our estimates and those cited in the literature for mean piglet weaning weight are not attributable to litter size since least-square purebred means are similar among studies. Differences in the breeds utilized for these studies could contribute to any parity differences reported here.

Previously reported comparisons of Yorkshire and Berkshire means for reproductive performance are limited. In addition, some litters contributing to the means reported by Johnson (1980) were from the Oregon State University herd and are used in this study. The mean number of purebred Yorkshire piglets born per litter are 10.22 (Young et al., 1976), 9.92 (Johnson and Omtvedt, 1973) and 10.81 (Johnson, 1980). Numbers at weaning also approximate the estimate reported in this study. Young et al. (1976) report mean number of piglets weaned of 7.42, Johnson and Omtvedt (1975) report 7.3 and Johnson (1980) reports 7.83 relative to our estimate of 8.14. The range among literature estimates for purebred Yorkshire birth weight is 1.01 kg (Johnson and Omtvedt, 1973) to 1.18 kg (Johnson, 1980). Literature estimates for mean piglet weaning weight are lower than estimates from this study, however, these literature estimates are for weaning at 42 days. Generally comparisons between the estimates calculated for this study are similar to those in the literature; differences which are noted could be attributable to differences in breeds used among studies or differences among management systems.

Young et al. (1976) and Johnson and Omtvedt (1973) use reciprocal crosses of Hampshire, Duroc and Yorkshire breeds to

estimate individual heterosis of .38 and .81 piglets per litter, respectively. For number of piglets born per litter, general combining abilities (Holtmann et al., 1975) evaluating crosses from 8 breeds of swine are 10.0 for the Yorkshire and 9.5 for the Berkshire breeds. Johnson (1980), utilizing 11 breeds, estimated individual heterosis to be .10 piglets per litter; this is a 1% increase in numbers born attributable to the crossbreeding of the piglets. Individual heterosis estimates from the literature range from 1% to approximately 10% for number born per litter; estimates from this study are 8% and 5% for nontransformed and transformed data, respectively.

Individual heterosis estimates for number weaned per litter are 1.06 (Johnson and Omtvedt, 1973) .76 (Young et al., 1976), .70 (Johnson, 1980), and .84 for this study; the expected increase in numbers weaned per litter range from 10% (Johnson, 1980) to 18% (Johnson and Omtvedt, 1973). Both numbers born alive and weaned per litter in this study, whether calculated as deviations from purebred means or as percents, approximate estimates reported in the literature.

Mean piglet birth weight estimates of individual heterosis are small but similar to estimates calculated in this study. Young et al. (1976) report increases of .014 kg, a 1% increase in mean piglet birth weight. Similarly, a .01 kg and .04 deviation for individual heterosis for piglet birth weight are reported by Johnson and Omtvedt (1973) and Johnson (1980), respectively. The estimate of .08 kg or 6% for this study is slightly higher than other individual heterosis estimates for mean piglet birth weight.

The transformed scale estimates individual heterosis for unadjusted mean piglet birth weight to be 23%; scales used by researchers cited in the literature utilize the nontransformed scale.

Adjusting mean piglet birth weight for litter size only slightly increases the percentage of individual heterosis for the nontransformed scale but nearly doubles the estimate for the transformed scale.

Weaning occurs at 42 days for the studies cited compared to 56 days for this study. This difference tends to enlarge deviations for individual heterosis between studies, and thus, estimates for comparison will be reported in percents. Johnson and Omtvedt (1973) report individual heterosis estimates for mean piglet weaning weight of 1%, Young et al. (1976) of 3% and Johnson (1980) of 5%. This study estimates individual heterosis for mean piglet weaning weight of 5% and 3% for nontransformed and transformed scales, respectively. Estimates for this study are similar to those previously reported by other researchers despite experimental differences in breeds utilized and days to weaning.

Nelson and Robison (1976), Johnson et al. (1978) and Johnson and Omtvedt (1975) report nonsignificant differences among mean maternal heterosis estimates for piglet birth and weaning weights for Yorkshire, Hampshire and Duroc crossbred dams. Johnson (1980), Johnson et al. (1978) and Johnson and Omtvedt (1975) report significant maternal heterosis effects for numbers weaned using two-breed crosses of dams. Johnson and Omtvedt (1975) and Nelson and Robison (1976) report nonsignificant differences among maternal heterosis estimates for numbers born per litter; Johnson (1980) and

Johnson et al. (1978) report significant maternal heterosis estimates for numbers born per litter. Deviations between crossbred and purebred dams for numbers born per litter are .93 (Johnson et al., 1978), .46 (Johnson, 1980), and .68 (Johnson and Omtvedt, 1975). Nontransformed differences for maternal heterosis in the present study are estimated at 1.03 for number of piglets born alive.

Estimates of maternal heterosis for numbers weaned per litter tend to be larger than estimates for number born per litter. Deviations of .58 (Johnson, 1980), 1.24 (Johnson et al, 1978), .98 (Johnson and Omtvedt, 1975) and 1.61 for this study are estimates of maternal heterosis for numbers weaned per litter. Maternal heterosis estimates for mean piglet birth weight do not attain significance and do not deviate from the mean by more than .06 kg. The effect of the crossbred dam on mean piglet birth weight is minimal and can be negative (Johnson and Omtvedt, 1975). Estimates of maternal heterosis for mean piglet weaning weight are negative and average -2.46 kg for this study. This result is not in agreement with estimates of 1.20 kg (Johnson, 1980), .02 kg (Johnson and Omtvedt, 1975) and .20 kg (Johnson et al, 1978). The negative maternal heterosis estimate for mean piglet weaning weight could be reflective of weaning at 56 days or the error involved calculating individual heterosis; the individual heterosis estimates are used in calculations of maternal heterosis estimates.

## SUMMARY

Purebred and crossbred Yorkshire and Berkshire breeds of swine were raised in complete confinement and evaluated for number born alive per litter, number weaned per litter, mean piglet birth weight and mean piglet weaning weight. A Composite breed, genetically equivalent to an F3 generation, was created from Berkshire X Yorkshire reciprocal crosses. Gilt and sow mean differences, breed means, paternal heterosis, maternal heterosis and individual heterosis are estimated on a Berkshire-Yorkshire basis.

Sow means exceed gilt means for number born alive and weaned per litter; differences are largest with the Berkshire breed, intermediate for the Composite breed and smallest for the Yorkshire breed. Purebred parity differences range from .00 kg to .11 kg for mean piglet birth weight and -0.49 kg to -2.88 kg for mean piglet weaning weight.

Purebred means for number born alive and weaned per litter are largest for Composites and smallest for the Berkshires; the reverse is true for mean piglet weaning weight. Piglet birth weights are low for Yorkshires and high for Berkshires.

Individual heterosis estimates are .71 and .84 for number born alive and weaned per litter, respectively. The individual heterosis estimate for mean piglet weight is .08 kg at birth and .81 kg at weaning. Estimates for percent increase in litter productivity attributable to the crossbred piglet range from 5% to

11%. All individual heterosis estimates are similar to those reported in the literature.

Crossbreeding of the dam positively influences number born and weaned per litter, has a slightly negative effect on mean piglet birth weight and a notable negative effect on mean piglet weaning weight. Since weights are not adjusted for litter size, negative estimates could reflect competition within a litter. All maternal heterosis estimates, except mean piglet weaning weight, are in agreement with reports from the literature. Maternal heterosis estimates are 1.0, 1.6,  $-.05$  kg, and  $-2.5$  kg for number born alive per litter, number weaned per litter, mean piglet birth weight and mean piglet weaning weight, respectively. Expressed as percents, heterosis for number born alive is 11%, for number weaned per litter is 22%, for mean piglet birth weight is  $-4\%$  and for mean piglet weaning weight is  $-16\%$ .

Paternal heterosis estimates calculated from Composite sires are  $-.94$  for number born alive per litter,  $.47$  for number weaned per litter,  $.17$  kg for mean piglet birth weight and  $-2.24$  kg for mean piglet weaning weight. On the average, the crossbred sire increases number weaned by 6% and mean piglet birth weight by 13%, but decreases number born alive by 10% and mean piglet weaning weight by 15%.

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HETEROSIS AND OTHER GENETIC PARAMETERS CALCULATED WITH  
ADDITIVE-DOMINANCE AND EPISTATIC MODELS

ABSTRACT

Purebred and crossbred litters of Yorkshire and Berkshire breeds of swine were evaluated for number of piglets born alive and weaned per litter and mean piglet birth and weaning weights (kg). The 632 litters consisting of two purebred and thirteen crossbred breed types were analyzed using a weighted least-squares analysis after adjustment to a sow equivalent. Weaning occurred at 56 days of age and piglets were exposed to feed from 14 days to weaning.

The additive-dominance model, a test for epistatic interactions, is not adequate for any trait examined ( $P < .001$ ). Fitting the two-locus epistatic model, a log base 10 scale is appropriate for number born alive ( $P = .05$ ) and weaned ( $P = .10$ ) per litter, mean piglet birth weight adjusted for litter size ( $P > .10$ ) and mean piglet weaning weight ( $P > .10$ ). The nontransformed data and epistatic model is appropriate ( $P > .10$ ) for mean piglet birth weight unadjusted for litter size. Parameters estimated are: the mean; maternal and litter additive effects; paternal, maternal and litter dominance; maternal epistatic interactions for additive X additive, additive X dominance, and dominance X dominance; and litter epistatic interactions for additive X additive, additive X dominance and dominance X dominance.

Berkshire additive effects and additive X dominance effects listed below should be multiplied by -1. Negative parameter estimates using the log transformed scale are  $-(\log \text{ estimate})$ ; these are not logs of negative numbers. Parameter estimates attaining statistical significance using the proper scale are listed below. For number born alive per litter, mean=1.375, maternal additive=.067, paternal dominance=-.185, litter dominance=-.568 and litter additive X additive=-.478. For number weaned per litter mean=1.343, maternal additive=.039, paternal dominance=-.187, litter dominance=-.511, and litter additive X additive=-.541. For mean piglet birth weight unadjusted for litter size, mean=.715, maternal additive=-.080, paternal dominance=.227, and maternal additive X additive=.248; no parameter estimates attain significance for mean piglet birth weight adjusted for litter size. For mean piglet weaning weight, mean=1.397, litter additive=-.041, maternal dominance=-.820 and maternal dominance X dominance=.597.

Marginal fits for number born alive and weaned per litter could be attributable to linkage, higher interactions, scale or interactions between parental and litter genotypes. These data do not permit testing for linkage or higher order interactions. The proper models and scales, however, can permit accurate estimation of breed means for untested breed types.

## INTRODUCTION

Crossbreeding is widely practiced in the livestock industry to maximize production through the use of heterosis. F1 crosses retain any beneficial effects from epistatic interactions and maximize the level of heterozygosity. F2 crosses and subsequent generations are expected to retain 1/2 the heterozygosity of the F1 yet can lose some epistatic effects as genetic combinations are broken up (epistatic or recombination loss). Few livestock studies have reported epistatic effects since large volumes of data are required.

This study i) evaluates the appropriateness of additive-dominance and two-locus epistatic interaction models for preweaning traits of Berkshire and Yorkshire crosses of swine, ii) evaluates scale effects, iii) estimates maternal and litter parameters for additive, dominance and epistatic interactions and iv) allows for prediction of production averages for crosses which have not yet occurred.

## MATERIALS AND METHODS

From 1967 to 1975, 632 litters of Berkshire, Yorkshire and 13 crosses embodying combinations of genes derived from them were produced; these are evaluated for number of piglets born alive per litter, number of piglets weaned per litter, mean piglet birth weight and mean piglet weaning weight. Lactating sows were fed 2.75 kg feed per day plus allowance of .0025 kg additional sow feed per day for each piglet. Piglets were weaned at 56 days post-parturition and had stater ration available from 14 days of age to weaning.

The 15 "breeds" (breed designates a unique mating), number of gilts and sows evaluated, means, and standard errors are in table 2.1. Breed means and standard errors for the transformed data (log base 10) are in table 2.2. Means in tables 2.1 and 2.2 are adjusted to a sow equivalent; standard errors are calculated from both gilt and sow variances. Mean piglet birth weight adjusted for number born alive per litter is calculated from the following formula.

$$\bar{x}_{bwa} = \bar{x}_{bw} - .0426 (\bar{x}_{nb} - \bar{x}_{nb})$$

where  $\bar{x}_{bwa}$  is the adjusted mean piglet birth weight

$\bar{x}_{nb}$  is the least-square grand mean for number of piglets born alive

TABLE 2.1. NUMBERS TESTED (N), MEANS AND STANDARD ERRORS (SE) WITH THE NONTRANSFORMED SCALE

Breed <sup>3</sup>	N <sup>1</sup>	Number born per litter		Number Weaned per litter		Piglet birth wt.-unadjusted (kg)		Piglet weaning wt. (kg)		Piglet birth wt.-adjusted Mean <sup>2</sup> (kg)
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean <sup>2</sup>
Berkshire (B)	8/40	7.90	.40	6.55	.35	1.429	.036	16.57	0.99	1.333
Yorkshire (Y)	35/80	10.70	.28	8.14	.26	1.210	.023	13.45	0.46	1.233
F3	20/41	10.71	.21	8.90	.24	1.292	.019	12.80	0.31	1.315
B X Y	7/12	10.58	.73	8.42	.76	1.275	.031	15.43	1.01	1.293
Y X B	1/16	9.44	.40	7.94	.39	1.495	.123	16.20	0.45	1.464
B X F3	13/4	10.25	.50	9.25	.59	1.279	.041	15.61	0.66	1.326
F3 X B	11/5	7.20	.44	7.00	.32	1.501	.083	15.29	1.04	1.375
Y X F3	9/14	9.93	.50	8.79	.54	1.264	.043	14.36	1.13	1.254
F3 X Y	14/6	11.17	.49	9.00	.46	1.356	.048	13.30	0.73	1.399
B X F1	6/15	9.87	.73	8.47	.62	1.347	.049	13.34	0.85	1.335
B{F3 X Y}	16/34	11.50	.46	9.32	.46	1.303	.046	12.73	0.47	1.360
Y X F1	17/29	11.10	.33	9.03	.35	1.400	.034	14.28	0.67	1.440
Y{B X F3}	28/67	9.55	.28	7.95	.29	1.390	.022	13.60	0.51	1.364
F3 X F1	14/24	11.75	.39	10.38	.38	1.361	.029	15.37	0.77	1.429
F2	13/33	9.76	.50	8.27	.40	1.471	.046	13.01	0.55	1.454

<sup>1</sup> Numbers for gilts/sows

<sup>2</sup> Standard errors utilized are those for the unadjusted birth weight

<sup>3</sup> The F3 is considered a Composite

TABLE 2.2. NUMBERS TESTED (N), MEANS AND STANDARD ERRORS (SE) WITH THE TRANSFORMED SCALE

Breed <sup>3</sup>	N <sup>1</sup>	Number born per litter		Number Weaned per litter		Piglet birth wt.-unadjusted (kg)		Piglet weaning wt. (kg)		Piglet birth wt.-adjusted (kg)
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean <sup>2</sup>
Berkshire (B)	8/40	0.862	.027	.778	.028	.150	.011	1.191	.022	.115
Yorkshire (Y)	35/80	1.002	.015	.873	.018	.072	.009	1.097	.015	.077
F3	20/41	1.020	.013	.934	.019	.106	.009	1.093	.015	.116
B X Y	7/12	1.001	.039	.895	.050	.103	.011	1.176	.031	.108
Y X B	1/16	0.956	.035	.877	.037	.169	.019	1.199	.026	.161
B X F3	13/4	0.980	.029	.956	.047	.104	.014	1.188	.020	.123
F3 X B	11/5	0.857	.024	.845	.020	.173	.023	1.171	.034	.137
Y X F3	9/14	0.984	.024	.924	.032	.097	.015	1.125	.033	.097
F3 X Y	14/6	1.042	.024	.943	.025	.129	.017	1.106	.023	.145
B X F1	6/15	0.956	.040	.892	.041	.154	.027	1.147	.044	.146
B{F3 X Y}	16/34	1.042	.022	.933	.033	.109	.011	1.091	.016	.125
Y X F1	17/29	1.033	.016	.931	.022	.141	.014	1.139	.019	.155
Y{B X F3}	28/67	0.956	.027	.875	.021	.137	.007	1.095	.018	.129
F3 X F1	14/24	1.060	.018	1.002	.018	.130	.009	1.165	.020	.151
F2	13/33	0.958	.029	.891	.026	.163	.012	1.099	.019	.155

<sup>1</sup> Numbers for gilts/sows

<sup>2</sup> Standard errors utilized are those for the unadjusted birth weight

<sup>3</sup> The F3 is considered a Composite

$\bar{x}_{nb}$  is the least-square breed mean for  
 number of piglets born alive

$\bar{x}_{bw}$  is the least-square breed mean for  
 mean piglet birth weight

Adjustment for the transformed data is performed with the same formula after substituting  $-.2811$  for  $-.0426$  and using transformed least-square grand and breed means.

An information matrix is created with breed expectations for an additive-dominance model (table 2.3) and a two-locus epistatic model (table 2.4). The six parameters estimated using the additive-dominance model are the mean, maternal and litter additive effects, and dominance effects attributable to paternal, maternal and litter sources. The epistatic model estimates parameters from additive-dominance model, as well as maternal and litter two-locus interactions for additive X additive, additive X dominance and dominance X dominance effects. Higher order interactions between three or more loci cannot be estimated from this data set.

Parameters are estimated with a weighted least-squares analysis (Mather and Jinks, 1971) using as weights the reciprocals of the squared standard errors. For each model, the 15 breed expectations (tables 2.3 and 2.4) are combined into a symmetrical matrix with a rank equal to the number of parameters being estimated. The system of simultaneous equations is solved to yield the parameters estimates. The general solution is:

TABLE 2.3. INFORMATION MATRIX FOR THE ADDITIVE-DOMINANCE MODEL

Breed	Mean	Additive		Dominance		
		Mat	Lit	Pat	Mat	Lit
Berk (B)	1	-1	-1	0	0	0
York (Y)	1	1	1	0	0	0
F3	1	0	0	1/2	1/2	1/2
B X Y	1	1	0	0	0	1
Y X B	1	-1	0	0	0	1
B X F3	1	0	-1/2	0	1/2	1/2
F3 X B	1	-1	-1/2	1/2	0	1/2
Y X F3	1	0	1/2	0	1/2	1/2
F3 X Y	1	1	1/2	1/2	0	1/2
B X F1	1	0	-1/2	0	1	1/2
B{F3 X Y}	1	1/2	-1/4	0	1/2	3/4
Y X F1	1	0	1/2	0	1	1/2
Y{B X F3}	1	-1/2	1/4	0	1/2	3/4
F3 X F1	1	0	0	1/2	1	1/2
F2	1	0	0	1	1	1/2

TABLE 2.4. INFORMATION MATRIX FOR THE EPISTASIS MODEL

Breed	Mean	Additive		Dominance			Epistasis <sup>1</sup>					
		Mat	Lit	Pat	Mat	Lit	Maternal			Litter		
-----	-----	-----	-----	-----	-----	-----	i	j	l	i	j	l
Berk (B)	1	-1	-1	0	0	0	1	0	0	1	0	0
York (Y)	1	1	1	0	0	0	1	0	0	1	0	0
F3	1	0	0	1/2	1/2	1/2	0	0	1/4	0	0	1/4
B X Y	1	1	0	0	0	1	1	0	0	0	0	1
Y X B	1	-1	0	0	0	1	1	0	0	0	0	1
B X F3	1	0	-1/2	0	1/2	1/2	0	0	1/4	1/4	-1/4	1/4
F3 X B	1	-1	-1/2	1/2	0	1/2	1	0	0	1/4	-1/4	1/4
Y X F3	1	0	1/2	0	1/2	1/2	0	0	1/4	1/4	1/4	1/4
F3 X Y	1	1	1/2	1/2	0	1/2	1	0	0	1/4	1/4	1/4
B X F1	1	0	-1/2	0	1	1/2	0	0	1	1/4	-1/4	1/4
B{F3 X Y}	1	1/2	-1/4	0	1/2	3/4	1/4	1/4	1/4	1/16	-3/16	9/16
Y X F1	1	0	1/2	0	1	1/2	0	0	1	1/4	1/4	1/4
Y{B X F3}	1	-1/2	1/4	0	1/2	3/4	1/4	-1/4	1/4	1/16	3/16	9/16
F3 X F1	1	0	0	1/2	1	1/2	0	0	1	0	0	1/4
F2	1	0	0	1	1	1/2	0	0	1	0	0	1/4

<sup>1</sup> i is the additive X additive interaction  
j is the additive X dominance interaction  
l is the dominance X dominance interaction

$$\hat{M} = J^{-1} S$$

where  $\hat{M}$  is the vector of estimated parameters  
 $J^{-1}$  is the inverted information matrix and the  
 variance-covariance matrix  
 $S$  is the vector of scores

If  $M$  is the number of breed types and if  $N$  is the number of parameters being estimated, the  $J$  matrix is a  $M \times N$  information matrix converted to a  $N \times N$  matrix before inversion (Mather and Jinks, 1971). The  $S$  vector is the vector of least-square breed means converted to a  $N \times 1$  vector in the same manner as the  $J$  matrix. Predicted breed means are calculated by multiplying the information matrix and the vector of estimated parameters ( $\hat{M}$ ) for each model. Adequacy of a model is tested with a chi-square goodness of fit with degrees of freedom (df) equal to 15 (number of breed types) minus the number of parameters being estimated. Initial analyses are performed by fitting the additive-dominance model to the nontransformed data. If the model is determined to be inadequate ( $P < .01$  with 9 df), the additive-dominance model is fitted to the transformed data. A poor fit for both data sets using the additive-dominance model requires fitting the epistatic model using first the nontransformed data followed by the transformed data. The process of fitting more complex models with nontransformed data and then transformed data is performed until an adequate fit ( $P > .05$ ) is determined. An example of this technique is presented by Mather and Jinks (1971, pg. 74). Statistical

significance of the estimated parameters is determined if twice the standard error subtracted from a positive estimate is greater than zero; negative parameters are significant if adding twice the standard error to the parameter results in a negative value.

## RESULTS

The standard errors of the slope estimates used for adjustment of mean piglet birth weight are .0151 and .1060 for nontransformed and transformed data, respectively. R-square values regressing mean piglet birth weight on number born alive are .34 for nontransformed data and .30 for transformed data. Associations between mean piglet weaning weight and number of piglets weaned per litter are not significant ( $P > .20$ ) and no adjustment to the data was applied.

### Additive-dominance model

Chi-square tests for adequacy of the additive-dominance model are highly significant ( $P < .01$ ) for all traits evaluated. Chi-squares with 9 df for nontransformed and transformed data, respectively, are 24.9 and 23.2 for number born alive per litter, 25.1 and 23.5 for number weaned per litter, 28.2 and 22.8 for mean piglet birth weight unadjusted for litter size, 22.2 and 17.4 for mean piglet birth weight adjusted for litter size, and 34.8 and 32.5 for mean piglet weaning weight.

All estimates for the mean are positive, significant and larger than additive and dominance estimates for all traits and scales examined. Regardless of scale, maternal additive and dominance estimates are significant, positive and larger than other additive or dominance estimates for number born alive and weaned per litter. Litter dominance estimates are positive for number born

and weaned per litter and are the only other parameter estimates which attain significance for these two traits. The maternal additive parameter is significant for the unadjusted mean piglet birth weight for both scales, and both paternal and litter dominance are positive and significant with the log base 10 scale. However, parameters for mean piglet birth weight adjusted for litter size are significant for maternal dominance with both scales and litter dominance is significant for the transformed data only. Additive parameter estimates are smaller than the dominance estimates for both scales evaluating adjusted mean piglet birth and weaning weight. For mean piglet weaning weight, all genetic parameter estimates, except the mean, are negative; maternal additive, paternal and litter dominance for the nontransformed and litter additive for the transformed scale are significant. Litter parameter estimates for nontransformed weaning weight are the least negative.

For comparison of predicted and actual breed means (sire X dam) for the additive-dominance model without the transformation, the Berkshire (B) X Yorkshire (Y), B X F1, and the F2 means are more than one piglet less than their predicted means for number born alive. The same three breed crosses are associated with the largest positive deviation when subtracting the actual mean from the predicted mean with the transformed scale. For number of piglets weaned per litter, B X Y and B X F1 predicted means exceed actual means while the reverse is true for the F3 X F1 cross. Actual unadjusted piglet birth weight means surpass the predicted mean for F3 sires mated to either Berkshire or Yorkshire dams;

however, the reciprocal cross means are lower than the predicted means with the nontransformed scale. The F3 breed mean is lower than predicted with both scales. Although the same trend persists with F3 crosses using the log base 10 transformation, F1 dams backcrossed to the purebreds exceed the predicted means.

Adjustment of mean piglet birth weight for litter size affects which breed is associated with the largest deviations between predicted and actual means. For both scales examined, Y X B and F3 X Y breeds exceed the predicted mean but the Y X F3 breed fails to attain the predicted level of production. The B X Y and the F3 X F1 exceed the predicted level for mean piglet weaning weight with both scales.

#### Epistatic model

Chi-square values identify the appropriate model and scale for estimation of the genetic parameters. For nontransformed and transformed scales respectively, chi-squares are >50 and 7.73 for number of piglets born alive per litter, 10.02 and 6.12 for number of piglets weaned per litter, 4.48 and 43.25 for mean piglet birth weight unadjusted for number born alive, 5.59 and 4.83 for adjusted mean piglet birth weight, 45.91 and 5.07 for mean piglet weaning weight. The appropriate scales for the epistatic model are log base 10 transformation for number born alive ( $.10 > P > .05$ ), number weaned ( $P > .10$ ), mean piglet weaning weight ( $P > .10$ ) and nontransformed scale for the unadjusted mean piglet birth weight ( $P > .10$ ). For number born alive and number weaned, P-values approach .05 and .10, respectively. Thus the epistatic model is

appropriate for birth and weaning weight, and marginally appropriate for number born alive and weaned per litter.

The number of piglets born alive and weaned per litter using log base 10 transformation is significantly influenced by the mean, maternal additive effects, paternal and litter dominance, and the litter additive X additive epistatic component. Significant paternal and litter estimates are negative. Disregarding sign, magnitude of the estimates decreases from litter estimates to paternal estimates with the maternal additive estimate being the smallest of the estimates attaining significance. For mean piglet birth weight, the nontransformed unadjusted data and the adjusted transformed and nontransformed data sets have similar chi-square values, and estimates attaining significance are dependent on scale and adjustment. For the nontransformed unadjusted data set which is associated with the lowest chi-square, the mean, maternal additive X additive, paternal dominance and the epistatic interaction between the maternal additive effects are statistically significant. The magnitude of the estimates in descending order are the mean, epistatic interaction, dominance, and the additive component. For the nontransformed adjusted mean piglet birth weight, only the mean and the maternal additive X additive estimates are significant; no estimates attain significance with the transformed data. For mean piglet weaning weight using the nontransformed scale, significant positive estimates exist for the mean and the maternal dominance X dominance, and significant negative estimates exist for litter additive and maternal dominance.

Comparison of the actual and predicted means for number born alive using the log base 10 scale are similar. Predicted means which exceed the actual mean by the largest deviation are for B X Y and B X F1 crosses. The Y X B breed mean cross has the largest positive deviation when subtracting the predicted mean from the actual mean. The same crosses and direction of deviations occur for the transformed number weaned per litter. The actual mean is greater than the predicted mean for the B X F3 cross for number weaned; however, the predicted mean is larger than the actual mean for number born alive. For mean piglet birth weight, subtracting the actual mean from the predicted mean shows large negative deviations for Y X B and Y X F1 crosses for nontransformed and adjusted data. For adjusted data, Y X B and B X F3 crosses are associated with the largest negative deviations, and the F3 X B and Y X F3 have large positive deviations. The actual mean for the B X F1 cross, which is associated with the largest predicted mean for mean piglet birth weight, does not approach or attain the predicted mean.

## DISCUSSION

To fully understand the parameter estimates, a brief discussion of the information matrices would be beneficial. The additive coefficients are the proportion of Berkshire and Yorkshire genes in the dam and litter. Litters and dams which are 100% Berkshire receive a coefficient of -1 while Yorkshire litters and dams receive a +1 coefficient. Coefficients for litter or dams containing both Berkshire and Yorkshire genes are calculated as the sum of  $[(+1)(\text{proportion of Yorkshire genes}) + (-1)(\text{proportion of Berkshire genes})]$ . Thus a dam or litter composed of 1/2 Yorkshire and 1/2 Berkshire genes is associated with a coefficient of zero  $[(+1)(1/2) + (-1)(1/2)]$ . The negative and positive one coefficients for each breed are set arbitrarily and do not affect calculation of the parameters; however, the coefficient's sign is important when calculating epistatic coefficients and predicting breed means. Dominance coefficients represent the proportion of loci within an individual expected to have one allele from each breed. These coefficients allow estimation of the magnitude of intra-locus interactions. Epistatic coefficients are products of the additive and dominance coefficients. The litter additive  $\times$  additive epistatic coefficient is the square of the litter additive coefficient; the litter additive  $\times$  dominance epistatic coefficient is the product of the litter additive and litter dominance coefficients. Thus, additive coefficients reflect the expected proportions of genes from each breed, dominance coefficients

reflect the proportion of loci containing alleles from each purebred breed, and epistatic coefficients are various products of the additive and dominance coefficients. Although the additive and dominance coefficients are used to estimate magnitudes of known genetic parameters, the epistatic coefficients, although easily calculated, are not easily interpretable. To give further meaning to the epistatic coefficients, the proportions of each litter and maternal genetic configuration considering a two-locus interaction model are presented in table 2.5. The genetic configurations for the B X F1 cross are given below:

<u>Sire</u>	<u>Dam</u>	<u>Litter</u>			
B1 B2	B1 B2	B1 B2	B1 B2	B1 B2	B1 B2
B1 B2	Y1 Y2	B1 B2	B1 Y2	Y1 B2	Y1 Y2

B = Berkshire allele

Y = Yorkshire allele

1 and 2 are loci

Since the B1-B1-B2-Y2 and the B1-Y1-B2-B2 cannot be differentiated with this analysis, the two configurations are represented as simply B-B-B-Y. Although no differences are acknowledged for B1-B1-B2-Y2 and B1-Y1-B2-B2 configurations, B1-B1-Y2-Y2 and B1-Y1-B2-Y2 are detectable and handled as separate configurations.

In table 2.4, the maternal and litter epistatic coefficients are shown and calculated as the products of additive and dominance

TABLE 2.5. CALCULATION OF TWO-LOCUS EPISTATIC COEFFICIENTS USING PROPORTIONS OF GENETIC CONFIGURATIONS

Breed	Expected proportions of genetic configurations <sup>1</sup>												Epistatic coefficients						
	Maternal						Litter						Maternal			Litter			
	Y1Y2	B1B2	B1Y2	Y1Y2	B1B2	B1B2	Y1Y2	B1B2	B1Y2	Y1Y2	B1B2	B1B2	i	j	l	i	j	l	
-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-	-	-	-	-	-	
Berk (B)	1						1						1						
York (Y)		1						1					1						
F3	1/16	1/16	1/8	1/4	1/4	1/4	1/16	1/16	1/8	1/4	1/4	1/4			1/4			1/4	
B X Y	1											1	1					1	
Y X B		1										1	1					1	
B X F3	1/16	1/16	1/8	1/4	1/4	1/4		1/4			1/2	1/4			1/4	1/4	-1/4	1/4	
F3 X B		1						1/4			1/2	1/4	1		1/4	-1/4	1/4	1/4	
Y X F3	1/16	1/16	1/8	1/4	1/4	1/4	1/4			1/2		1/4			1/4	1/4	1/4	1/4	
F3 X Y	1						1/4			1/2		1/4	1		1/4	1/4	1/4	1/4	
B X F1						1		1/4			1/2	1/4			1	1/4	-1/4	1/4	
B(F3 X Y)	1/4			1/2		1/4		1/16				3/8	9/16	1/4	1/4	1/4	1/16	-3/16	9/16
Y X F1						1	1/4				1/2	1/4			1	1/4	1/4	1/4	
Y(B X F3)		1/4			1/2	1/4	1/16				3/8		9/16	1/4	-1/4	1/4	1/16	3/16	9/16
F3 X F1						1	1/16	1/16	1/8	1/4	1/4	1/4			1			1/4	
F2						1	1/16	1/16	1/8	1/4	1/4	1/4			1			1/4	
Column	1	2	3	4	5	6	7	8	9	10	11	12							

<sup>1</sup> numbers represent loci and letters represent breed of origin

coefficients. A second method of calculation for the epistatic coefficients, and perhaps more interpretable, uses linear combinations of columns in table 2.5. The maternal additive X additive (i) coefficient represents column 1 + column 2 - column 3. The maternal additive X dominance (j) coefficient is calculated as (column 4 - column 5)/2; the maternal dominance X dominance coefficient is identical to column 6. Likewise for the litter coefficients, i is equal to column 7 + column 8 - column 9; j equals (column 10 - column 11)/2; and l equals column 12. Thus the epistatic coefficients are reflective of the linear combinations of expected genetic configurations.

The grouping of columns does have meaning. Taking the maternal configurations, columns 1-3 are loci that are "homozygous" considering breed of origin and the estimation is termed the homozygous X homozygous or additive X additive epistatic interaction. Similarly, columns 4 and 5 are homozygous at one locus and heterozygous at the other and are referred to as the additive X dominance interaction, and column 6 is the dominance X dominance interaction. The signs associated with the linear contrasts also have some meaning. Columns 1 and 2 of the additive X additive interaction have a positive coefficient which reflects inter-locus interactions among alleles from the same breed of origin; column 3 associated with a negative coefficient, represents interactions of alleles from different breeds of origin. The additive X dominance interactions contain three alleles from one breed and one allele from the second breed; the sign of the

coefficient in columns 4 and 5 reflects the arbitrary assignment of -1 and +1 to the breed with 3 alleles in the genetic configuration.

The use of both nontransformed and transformed scales to evaluate genetic parameters is best supported by example.

		Locus 1		
		YY	YB	BB
Locus 2	YY	1/.000	2/.301	3/.477
	BY	2/.301	4/.602	6/.778
	BB	3/.477	6/.778	9/.954

(adapted from Mather and Jinks, 1971)

The numbers in the matrix represent phenotypic means on the nontransformed and log base 10 transformed (upper/lower) scales. Y and B represent alleles from Yorkshire and Berkshire origins, respectively. Using the nontransformed (upper) scale, dominance is not present since the heterozygote is intermediate to the homozygotes for both loci; however, epistasis is present. The presence of epistatic interactions is determined if each phenotypic mean does not equal the grand mean plus a row and column mean expressed as a deviation from the grand mean. Using the transformed scale, dominance is present (B is incompletely dominant to Y) since the heterozygote is not intermediate to the homozygotes yet epistasis is not present. Thus two completely different conclusions can be reached with identical data sets using two different scales.

Our analysis attempts to fit the simplest model to a scale which adequately describes the breed means; if such a scale is not found, a more complex model is utilized. If an adequate model and scale are not found, then linkage or higher order interactions theoretically should be tested; our data do not permit testing for linkage or higher order interactions. To test higher order interactions, more breeds must be tested to allow for sufficient degrees of freedom to test the adequacy of the model; there must be more breed means than parameters estimated. Also this particular technique is only appropriate for crosses originating from two breeds although techniques which allow for more breeds combinations do exist (Kinghorn, 1980).

The amount of empirical evidence in the literature for epistatic interactions in livestock is sparse. McGloughlin (1980), with two genetically diverse lines of mice, states that a linear relationship exists between heterosis and heterozygosity and that no epistatic or recombination losses are apparent with the same characters examined in this study. Kinghorn (1982), using three strains of mice and evaluating reproductive traits and body measurements, concludes that the additive X additive interaction model is most appropriate. He further concludes that "hypothesis X" (Kinghorn, 1980) should be assumed when analyzing data for heterosis. Hypothesis X is analogous to forming a dimeric enzyme where epistatic (or recombinant) loss is "proportional to the probability that two non-allelic genes randomly chosen in a diploid individual are of different breed origin." Using hypothesis X, epistatic loss coefficients for additive X dominance

and dominance X dominance interactions would be 1/2. The epistatic loss (e) used by Kinghorn (1980) and recombinant loss (r) used by Dickerson (1973) are related by:

$$r = 2(\text{coefficient for } e) - \text{coefficient for individual heterosis (Koch et al., 1985)}$$

No evidence of epistatic effects was found by Koch et al. (1985) with beef cattle or by Robison et al. (1981) with dairy cattle. Dillard et al. (1980) conclude that differences for weaning weight and average daily gain might be affected by epistasis or linkage but that these differences account for only 1% of the total variation. Rastogi et al. (1982) report some small but favorable recombination effects for weights at birth, weaning, and postweaning average daily gain for lambs from Columbia, Suffolk and Targhee breeds of sheep. Sheridan (1981) and Koch et al. (1985) cite reports in which interactions may have gone undetected by the authors by comparing backcross means with F2 means. Assuming that litter additive, paternal dominance and epistatic interactions are negligible, means of backcrosses and the F2 should be approximately equal. Evaluation of F1 and F2 means (Sheridan, 1981) between four inbred lines of White Leghorns for egg production reveals that the F2 population retains less than 1/4 of the heterosis expressed in the F1. The F2 population would be expected to have 1/2 the heterosis of the F1 if epistatic interactions were not important.

Interpretation of the genetic parameters is appropriate only when the adequacy of a model and scale have been determined. The

additive-dominance estimates and some inappropriate epistatic model scales are mentioned to illustrate the differences among estimates. In the present study of number born alive and weaned per litter, maternal additive and dominance and litter dominance are significant and positive with the additive-dominance model. Other than for the mean, the maternal additive component is the only significant and positive estimate fitting the epistatic model; paternal and litter dominance and the litter additive interaction are significant and negative. For the epistatic model estimates for mean piglet birth weight unadjusted for litter size, the maternal additive estimate is significant and negative for the nontransformed data but positive for the log base 10 data. For adjusted mean piglet birth weight and mean piglet weaning weight comparisons within scale, no two estimates of parameters other than the mean attain significance. Some differences between models exist due to differences in precision between models with nine and three degrees of freedom. Both scale and model must be adequate before breeding plans are determined using these parameter estimates.

When the best model and appropriate scale are identified and shown to adequately predict the least-squares breed means, interpretation of the parameter estimates is necessary. The additive X additive estimate is a combination of the two purebred genetic configurations and a configuration represented by one locus with two alleles from the Berkshire breed and the second locus with alleles from the Yorkshire breed (table 2.5). Breakup of the purebred configurations has been referred to as epistatic loss

(Kingham, 1980) or recombination loss (Dickerson, 1969).

Splitting of gene combinations containing alleles from the same breed of origin is not limited to a loss in production. Species, breeds or lines subjected to prolonged artificial selection for a particular trait would probably display a loss in production reflecting the loss of favorable epistatic effects in the crossbreds (>F1). The maternal additive X dominance interaction is difficult to estimate with our data since in all but two breeds of dam, either the genetic configurations are not present or the BBBY and the YYYY configurations negate each other's effects (table 2.4) This situation does not exist with the litter additive X dominance interaction. The dominance X dominance interaction is reflective of interaction between two "heterozygous" loci.

For number born alive and weaned per litter, the same set of parameter estimates attain significance (table 2.6). Dominance estimates for both litter and paternal components are negative suggesting the purebreds may be preferred; however, the litter additive X additive estimate is also negative. Thus there is a balance between the crossbreds having a loss in performance due to crossbred sires and dams, yet the purebreds having a loss in number born and weaned due to an epistatic effect in the litters. Dwarfed by the mentioned estimates, yet attaining significance, is the maternal additive component. Considering all parameter estimates for number born and weaned per litter, the estimates would suggest some additive genetic variation still exists although dominance and litter additive epistatic effects are more influential. For number born alive per litter (table 2.7), the most prolific breeds are the

TABLE 2.6. PARAMETER ESTIMATES (EST) AND STANDARD ERRORS (SE) FOR A TWO-LOCUS MODEL USING THE BEST SCALE

Parameter <sup>1</sup>	Number born alive per litter (Log base 10)		Number Weaned per litter (Log base 10)		Mean piglet birth weight-unadjusted (Nontransformed) (kg)		Mean piglet birth weight-adjusted (Log base 10) (kg)		Mean piglet weaning weight (Log base 10) (kg)	
	EST	SE	EST	SE	EST	SE	EST	SE	EST	SE
Mean	1.375	.139	1.343	.152	.715	.217	.036	.067	1.397	.119
Maternal add	.067	.017	.039	.019	-.080	.040	-.016	.009	-.006	.016
Litter add	.003	.023	.008	.025	-.027	.046	-.004	.011	-.041	.020
Dominance										
Paternal	-.185	.064	-.187	.061	.227	.104	.006	.029	-.089	.051
Maternal	-.052	.277	-.180	.333	.508	.424	.042	.119	-.820	.214
Litter	-.568	.227	-.511	.254	.701	.383	.163	.127	.046	.221
Maternal epistasis										
add X add	.035	.112	.024	.135	.248	.123	.059	.052	-.216	.299
add X dom	.058	.089	.038	.106	-.013	.142	.026	.040	-.070	.071
dom X dom	.069	.181	.161	.216	-.248	.277	.023	.078	.597	.138
Litter epistasis										
add X add	-.478	.160	-.541	.169	.362	.256	.002	.079	-.037	.144
add X dom	.023	.053	-.011	.059	.033	.104	.008	.033	-.046	.054
dom X dom	.143	.114	.039	.126	-.298	.216	-.129	.073	-.039	.117

<sup>1</sup> add and dom represent additive and dominance, respectively

TABLE 2.7. ACTUAL (Act) AND ESTIMATED (Est) BREED MEANS WITH A TWO-LOCUS MODEL AND THE BEST SCALE

Breed	Number born per litter (Log base 10)		Number Weaned per litter (Log base 10)		Piglet birth wt.-unadjusted (Nontransformed) (kg)		Piglet birth wt.-adjusted (Log base 10) (kg)		Piglet weaning wt. (Log base 10) (kg)	
	Act	Est	Act	Est	Act	Est	Act	Est	Act	Est
Berk (B)	0.862	0.862	0.778	0.778	1.432	1.429	0.115	0.115	1.191	1.191
York (Y)	1.002	1.002	0.873	0.973	1.218	1.210	0.077	0.077	1.097	1.097
F3	1.025	1.020	0.954	0.934	1.297	1.292	0.115	0.116	1.105	1.093
B X Y	1.051	1.001	0.934	0.895	1.286	1.275	0.113	0.108	1.182	1.176
Y X B	0.917	0.956	0.856	0.877	1.446	1.495	0.144	0.161	1.195	1.199
B X F3	0.991	0.980	0.911	0.956	1.279	1.279	0.112	0.123	1.172	1.188
F3 X B	0.875	0.857	0.852	0.845	1.528	1.501	0.162	0.137	1.179	1.171
Y X F3	1.006	0.984	0.914	0.924	1.268	1.264	0.112	0.097	1.109	1.125
F3 X Y	1.023	1.042	0.933	0.943	1.358	1.356	0.132	0.145	1.103	1.106
B X F1	1.017	0.956	0.941	0.892	1.347	1.347	0.150	0.146	1.211	1.147
B{F3 X Y}	1.042	1.042	0.933	0.933	1.307	1.303	0.125	0.125	1.091	1.091
Y X F1	1.031	1.033	0.944	0.931	1.336	1.400	0.150	0.155	1.147	1.139
Y{B X F3}	0.956	0.956	0.875	0.875	1.392	1.390	0.129	0.129	1.095	1.095
F3 X F1	1.051	1.060	0.984	1.002	1.365	1.361	0.153	0.151	1.143	1.165
F2	0.958	0.958	0.891	0.891	1.478	1.471	0.155	0.155	1.099	1.099

B(F3 X Y), F3 X Y, and the F3 X F1. The latter two breeds are predicted by the model to be the most prolific. The purebred Berkshire and the F3 X B are the poorest breeds examined for number born alive. For number weaned per litter, predicted means for breeds representing the highest and lowest producers are similar to the actual means. The F3 X F1 breed produces the most piglets at weaning while the purebred Berkshire and F3 X B have the fewest piglets at weaning.

For nontransformed mean piglet birth weight unadjusted for litter size (table 2.6), significant maternal additive, maternal additive X additive and paternal dominance components are identified. As might be expected, the signs of significant components are opposite the same components for number born per litter. The predicted and actual breed means, which are associated with the largest mean piglet birth weights (table 2.7), are the same breeds associated with fewest born alive per litter. In addition to both the purebred Berkshire and the F3 X B, which have fewest piglets per litter but a high mean piglet birth weight, the F2 and the Y X B produce litters with large piglets as predicted by the model. The Y X F3 and purebred Yorkshire predicted and actual means are the lowest among the breeds evaluated for mean piglet birth weight.

Only the estimated mean for the adjusted and transformed mean piglet birth weight attain significance (table 2.6). The largest estimates are associated with the F1 dams and the F2 breed (table 2.7). Purebred Yorkshires, as predicted, are the breed with the lowest mean piglet birth weight utilizing the best fitting model

and scale. The mean, maternal dominance, the epistatic estimate for maternal dominance X dominance and litter additive estimates are significant for mean piglet weaning weight. Again a balance is apparent where the maternal dominance estimate is negative and the dominance X dominance maternal epistatic interaction is positive. Furthermore the litter additive component attains significance, yet the magnitude of the estimate is less than 1/10 that of the other significant components. There appears to be some available genetic variation in the litter from which to select, yet relative to other components, the additive source is minute. Predicted and actual breed means are similar for weaning weight except the B X F1 cross where the predicted mean exceeds the actual mean. The breeds with the highest means are the purebred Berkshire dams mated to a Berkshire or Yorkshire sire. A group of breeds associated with the lowest mean piglet weaning weight are the purebred Yorkshire, F2, F3, B(F3 X Y) and the Y(B X F3).

Estimates obtained using the additive-dominance model are inaccurate, biased and not appropriate for this data, however, the estimates do have interest. Assuming the epistatic effects are negligible for number born alive and number weaned per litter, maternal additive, maternal dominance and litter dominance estimates are large and positive. Likely conclusions are the trait is moderately heritable and that a positive association exists between hybrid vigor and number born and weaned per litter. Genetic response to these traits would be expected if proper selection procedures were employed. Conversely, conclusions utilizing the epistatic model would be that the trait is lowly

heritable and hybrid vigor tends to decrease litter size at birth and weaning. Despite being similar in magnitude, generally differences between estimates obtained with the two models are universal for the traits examined; relative to other genetic parameter estimates, the maternal additive estimates tend to be large with the additive-dominance model and relatively small with the epistatic model. Large maternal additive estimates relative to dominance and epistatic estimates would imply adequate additive variation exists for selection to be successful and the heritability would be expected to be moderate to high. Small maternal additive estimates relative to the other genetic parameters would imply less available additive genetic variation and a lower heritability. The parameter estimates from the two-locus interaction model and best scale would suggest that artificial selection would not lead to substantial herd improvement and evaluation of epistatic effects would produce more immediate progress. If selection were to be incorporated in a long range herd improvement program, single-trait selection would be best performed on the dam for all traits examined except mean piglet weaning weight. Using single-trait selection, more genetic improvement can be made by selecting for the litter or dam with the largest additive component; selection in both the litter and dam would be expected to be more successful than selecting in either the litter or dam.

The assumptions of our analysis include no linkage and no interaction between maternal, paternal or litter genotypes. Tests for particular scales and the two-locus interaction model were

determined to be nonsignificant ( $P > .05$ ); however, other scales and models may more accurately estimate least-square breed means. Linkage, higher order interactions, interactions among parental and litter genotypes and scale may all be tested with the appropriate data. This data can be used only to evaluate scales, additive-dominance and two-locus models, and interactions among genotypes. The estimates for number born alive and weaned per litter are adequate but marginal. Linkage, higher order interactions, interactions among parental and litter genotypes, and scale could contribute to the marginal fit.

Our analyses allow for estimation of genetic parameters and estimation of predicted means of crosses not yet performed. Differences between actual and predicted means with the best fitting models and scales for number born alive and weaned per litter are less than 6% for all breeds. Except for the B X F1 cross, where actual and predicted means differ by 6% and 5% for number born alive and number weaned respectively, most differences are 2% or less. Except for the B X F1 cross, differences for mean piglet weaning weight between predicted and actual means are small. All differences between actual and predicted means are less than 5% for mean piglet birth weight unadjusted for litter size. The largest difference between means for unadjusted means piglet birth weight is for the Y X F1 cross. The largest discrepancies between predicted and actual means occur for the transformed mean piglet birth weight adjusted for litter size. These differences may be attributable to rounding error or the adjustment for litter size.

The model appropriate for these data is a two-locus epistatic interaction model which estimates 12 genetic parameters. These parameters are used to calculate predicted least-square breed means adjusted to a sow equivalent. The models are tested for adequacy using a chi-square comparing actual and predicted means. The largest difference between actual and predicted means for unadjusted data is 6%; most differences are less than 2%. This model and the parameters estimated can be used to establish breeding plans and predict breed means before the breeding occurs. Genetic interactions not occurring in breeds included in the analysis or new genetic combinations may not allow for accurate prediction. However, assuming the same set of genes and interactions are present in a cross not tested, prediction of a mean for an untested breed should be accurate.

## SUMMARY

Data from 632 litters of crossbred and purebred Yorkshire and Berkshire breeds of swine are evaluated for number born alive per litter, number weaned per litter, mean piglet birth weight, mean piglet weaning weight, and mean piglet birth weight adjusted for litter size. Least-square means of 13 crossbred and 2 purebred types of breeding are used in a weighted least-squares analysis to estimate the following parameters: the mean, maternal and litter additive effects; maternal, paternal and litter dominance; maternal epistatic interactions between additive X additive, additive X dominance, and dominance X dominance components; and litter epistatic interactions between additive X additive, additive X dominance, and dominance X dominance components.

Additive-dominance and two-locus epistatic models are tested for adequacy with nontransformed and log base 10 transformed scales.

The additive-dominance model is not adequate ( $P < .001$ ) for any trait or scale examined. The two-locus epistatic model is adequate for transformed number piglets born alive per litter ( $P = .05$ ), transformed number piglets weaned per litter ( $P = .10$ ), nontransformed unadjusted mean piglet birth weight ( $P > .10$ ), and transformed mean piglet weaning weight ( $P > .10$ ). The marginal fit of the epistatic model for number born alive and weaned per litter could be attributable to linkage, higher order interactions, scale, or interactions between parental and litter genotypes.

Assuming no epistatic interactions falsely suggests that the maternal additive component is important relative to other estimates; the epistatic model reveals that the maternal additive component is not as large in magnitude as other genetic parameters. Assuming no epistatic interactions suggests a moderate heritability; however, using the correct epistatic model suggests a low heritability. The parameter estimates for litter additive are only important for mean piglet weaning weight.

Predicted means for the 15 breed types are generally within 5% or less of the actual least-square breed means. Assuming no new genetic combinations or interactions would be present in crosses not yet formed, breeding plans could optimize the use of important beneficial genetic components, minimize the influences of the negative components and accurately predict breed average production before matings occur.

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## CONCLUSIONS

Comparison of Yorkshire breed means for number born alive and weaned per litter are slightly higher than literature estimates. Berkshire means for number born alive and weaned per litter tend to be slightly lower than the limited number of reports in the literature. For mean piglet birth and weaning weights, estimates from our study are similar to those in the literature. Thus, the purebred Berkshire and Yorkshire pigs utilized in our study have phenotypically similar reproductive performance levels as those reported in the literature.

Individual heterosis estimates for number born and weaned per litter, expressed as a deviation with the nontransformed scale or as a percent with either scale, approximate the estimates in the literature. Nontransformed individual heterosis estimates for mean piglet birth weight are slightly larger than literature reports; the percent of individual heterosis based on the transformed scale is nearly four fold greater than the nontransformed data estimate. Individual heterosis estimates for mean piglet birth weight adjusted for litter size exceed estimates which are not adjusted. Comparisons of literature estimates of individual heterosis for weaning weight approximate the estimates for our study despite management and breed differences. Maternal heterosis estimates for number born and weaned per litter are slightly larger than literature estimates. For piglet birth weight, literature estimates and our estimates are similar and both approximate zero.

For mean piglet weaning weight, our estimates are negative and differ from literature estimates; these differences might result from our longer preweaning period or to differences among breeds utilized in the studies. In general, estimates of breed effects and heterosis calculated in this study are within the range reported in the literature; the pigs used in our study do not appear to differ significantly from those tested elsewhere.

Estimating litter heterosis assuming no epistasis (chapter 1) is similar to estimating litter dominance with the additive-dominance model (chapter 2). Expressing the difference between estimates in standard error units calculated from the additive-dominance model can describe the degree to which the estimates differ. Differences between estimates assuming no epistasis and using the additive-dominance model expressed in standard error units for number born alive per litter are .65 and .16 for nontransformed and transformed data, respectively. For mean piglet weaning weight, differences between estimates are .68 and .71 standard error units for nontransformed and transformed data, respectively. For the nontransformed data, estimate differences in standard error units are 1.09, 1.52 and 1.80 for mean piglet birth weight unadjusted for litter size, birth weight adjusted for litter size and mean piglet weaning weight, respectively; the same estimates for the transformed data are .26, .11 and 2.62, respectively. Differences between individual heterosis estimates are not significant except nontransformed mean piglet birth weight adjusted for litter size and nontransformed mean piglet weaning weight. These differences in standard error

units are similar to testing an estimates's statistical significance from zero as opposed to testing differences between two estimates.

Nontransformed maternal heterosis differences between the additive-dominance model and the model assuming no epistasis in standard error units are 1.28 for number born alive, 1.17 for number weaned, 2.45 for unadjusted mean piglet birth weight, 3.07 for adjusted mean piglet birth weight and 3.17 for mean piglet weaning weight. For the transformed data, maternal heterosis estimate differences in standard error units are 1.38 for number born alive, 1.47 for number weaned per litter 1.10 for unadjusted mean piglet birth weight, 1.50 for adjusted mean piglet birth weight and 3.94 for mean piglet weaning weight. Thus differences between model estimates for maternal heterosis tend to be small.

Paternal heterosis differences between model estimates in standard error units for the nontransformed data are 1.68 for mean number piglet born alive, 1.59 for mean number piglets weaned, 4.09 for unadjusted mean piglet birth weight, 2.12 for adjusted mean piglet birth weight and 1.98 for mean piglet weaning weight. Estimates for the transformed data are .38 for number born alive per litter, 2.35 for number weaned per litter, 2.33 for unadjusted mean piglet birth weight, 2.42 for adjusted mean piglet birth weight and 1.37 for mean piglet weaning weight. As with model differences expressed in standard error units for individual and maternal heterosis, differences tend to be small.

Transformed standard error estimates with the epistatic model are 11, 14 and 3 times the standard error estimates for the

additive-dominance model for litter, maternal and paternal heterosis, respectively. Comparing estimates from the epistatic model with other model estimates using standard errors from the epistatic model would generally not show differences among estimates. Comparison of estimates between the epistatic model and appropriate scale with those estimated from chapter 1 may be informative. Using the appropriate scale from chapter 2, comparison of epistatic model estimates for individual, maternal and paternal heterosis to those of chapter 1 are given. The antilog of the log transformed estimates is used when the log 10 scale is determined to be the appropriate scale. The estimates for the model assuming no epistatic interactions and the epistatic model, respectively, are listed below: for number born alive per litter, litter heterosis estimates are 1.11 and -3.70, maternal heterosis estimates are 1.13 and -1.13, and paternal heterosis estimates are -1.03 and -1.53; for number weaned per litter, litter heterosis estimates are 1.15 and -3.24, maternal estimates are 1.25 and -1.51, and paternal heterosis estimates are 1.19 and -1.54; for unadjusted mean piglet birth weight, litter heterosis estimates are .08 kg and .70 kg, maternal heterosis estimates are -.05 kg and .51 kg, and paternal heterosis estimates are .17 kg and .23 kg; for adjusted mean piglet birth weight, litter heterosis estimates are 1.09 kg and 1.46 kg, maternal heterosis estimates are 1.02 kg and 1.10 kg, and for paternal heterosis estimates are 1.12 kg and .00 kg; for mean piglet weaning weight, litter heterosis estimates are 1.11 kg and 1.11 kg, maternal heterosis estimates are -1.17 kg and -6.61 kg, and paternal heterosis estimates are -1.14 kg and -1.23

kg. Differences between estimates are most notable for litter and maternal heterosis estimates for number born and weaned per litter; positive estimates are associated with models not assuming epistasis while large negative estimates are associated with estimates for the epistatic model. Paternal heterosis estimates follow the same pattern for number weaned per litter. Litter heterosis estimates for birth weight tend to be larger with the epistatic interaction model than models assuming no interactions. Paternal heterosis estimates are positive for adjusted mean piglet birth weight assuming no interactions; however, the estimate is zero when epistatic interactions are included in the model. For mean piglet weaning weight, maternal heterosis estimates are negative with both models; the differences between estimates amount to almost 5.5 kg. Thus for each trait evaluated, there is at least one estimate of heterosis which considerably differs between models considering or not considering epistatic interactions. Furthermore, these comparisons are based upon the scale which is found to be the most appropriate; this is not the scale generally utilized in analyses in the literature.

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## APPENDIX

TABLE A1. ESTIMATES OF THE MEAN, MATERNAL ADDITIVE, LITTER ADDITIVE, PATERNAL DOMINANCE, MATERNAL DOMINANCE, LITTER DOMINANCE AND STANDARD ERRORS FITTING THE ADDITIVE-DOMINANCE MODEL

Number piglets born alive per litter

Parameter	Nontransformed		Transformed ( $\log_{10}$ )	
	Estimate	SE <sup>1</sup>	Estimate	SE <sup>1</sup>
Mean	9.29	0.23	.936	.014
Maternal additive	1.56	0.23	.072	.013
Litter additive	-0.14	0.28	-.002	.016
Paternal dominance	-0.32	0.37	-.004	.021
Maternal dominance	1.40	0.29	.074	.016
Litter dominance	0.97	0.40	.051	.025

<sup>1</sup> Standard Error

TABLE A2. ESTIMATES OF THE MEAN, MATERNAL ADDITIVE, LITTER ADDITIVE, PATERNAL DOMINANCE, MATERNAL DOMINANCE, LITTER DOMINANCE AND STANDARD ERRORS FITTING THE ADDITIVE-DOMINANCE MODEL

Number piglets weaned per litter

Parameter -----	Nontransformed <sup>1</sup>		Transformed (log <sub>10</sub> )	
	Estimate	SE <sup>1</sup>	Estimate	SE <sup>1</sup>
-----	-----	-----	-----	-----
Mean	7.47	0.21	.839	.015
Maternal additive	1.02	0.22	.048	.015
Litter additive	-0.30	0.27	-.008	.020
Paternal dominance	-0.07	0.34	.022	.023
Maternal dominance	1.29	0.27	.072	.017
Litter dominance	1.10	0.38	.067	.028

<sup>1</sup> Standard Error

TABLE A3. ESTIMATES OF THE MEAN, MATERNAL ADDITIVE, LITTER ADDITIVE, PATERNAL DOMINANCE, MATERNAL DOMINANCE, LITTER DOMINANCE AND STANDARD ERRORS FITTING THE ADDITIVE-DOMINANCE MODEL

Parameter	Nontransformed <sup>1</sup>		Transformed (log <sub>10</sub> )	
	Estimate	SE <sup>1</sup>	Estimate	SE <sup>1</sup>
Mean	1.299	.020	.107	.007
Maternal additive	-0.085	.020	-.029	.006
Litter additive	-0.001	.023	-.005	.007
Paternal dominance	0.031	.034	.027	.012
Maternal dominance	0.020	.029	.001	.010
Litter dominance	0.044	.033	.021	.010

<sup>1</sup> Standard Error

TABLE A4. ESTIMATES OF THE MEAN, MATERNAL ADDITIVE, LITTER ADDITIVE, PATERNAL DOMINANCE, MATERNAL DOMINANCE, LITTER DOMINANCE AND STANDARD ERRORS FITTING THE ADDITIVE-DOMINANCE MODEL

Mean piglet birth weight (kg) adjusted for  
number piglets born alive per litter

Parameter	Nontransformed		Transformed ( $\log_{10}$ )	
	Estimate	SE <sup>1</sup>	Estimate	SE <sup>1</sup>
Mean	1.268	.020	.095	.007
Maternal additive	-0.025	.020	-.011	.006
Litter additive	-0.004	.023	-.006	.007
Paternal dominance	0.038	.034	.022	.012
Maternal dominance	0.090	.029	.025	.010
Litter dominance	0.050	.033	.028	.010

<sup>1</sup> Standard Error

TABLE A5. ESTIMATES OF THE MEAN, MATERNAL ADDITIVE, LITTER ADDITIVE, PATERNAL DOMINANCE, MATERNAL DOMINANCE, LITTER DOMINANCE AND STANDARD ERRORS FITTING THE ADDITIVE-DOMINANCE MODEL

Mean piglet weaning weight (kg)

Parameter	Nontransformed		Transformed (log <sub>10</sub> )	
	Estimate	SE <sup>1</sup>	Estimate	SE <sup>1</sup>
Mean	14.76	0.46	1.146	.012
Maternal additive	-1.12	0.31	-.019	.011
Litter additive	-0.24	0.43	-.029	.014
Paternal dominance	-1.19	0.53	-.029	.019
Maternal dominance	-0.94	0.48	-.007	.016
Litter dominance	-0.23	0.66	-.011	.021

<sup>1</sup> Standard Error

TABLE A6. PREDICTED BREED MEANS, ACTUAL BREED MEANS, AND CHI SQUARE GOODNESS OF FIT TEST USING THE ADDITIVE-DOMINANCE MODEL

Breed <sup>1</sup>	Number piglets born alive per litter		Number piglets born alive per litter	
	Nontransformed means Predicted	Actual	Transformed means (log 10) Predicted	Actual
Berk (B)	7.88	7.90	0.866	0.862
York (Y)	10.71	10.70	1.006	1.002
F3	10.32	10.71	0.977	1.020
B X Y	11.83	10.58	1.059	1.001
Y X B	8.71	9.44	0.916	0.956
B X F3	10.55	10.25	1.000	0.980
F3 X B	8.13	7.20	0.889	0.857
Y X F3	10.41	9.93	0.998	0.984
F3 X Y	11.11	11.17	1.030	1.042
B X F1	11.26	9.87	1.037	0.956
B{F3 X Y}	11.54	11.50	1.048	1.042
Y X F1	11.12	11.10	1.035	1.033
Y{B X F3}	9.91	9.55	0.975	0.956
F3 X F1	11.03	11.75	1.034	1.060
F2	10.86	9.76	1.032	0.958
Chi square	24.87		23.18	

<sup>1</sup> Breed pertains to breed of litter

TABLE A7. PREDICTED BREED MEANS, ACTUAL BREED MEANS, AND CHI SQUARE GOODNESS OF FIT TEST USING THE ADDITIVE-DOMINANCE MODEL.

Breed <sup>1</sup>	Number piglets weaned per litter		Number piglets weaned per litter	
	Nontransformed means Predicted	Actual	Transformed means (log 10) Predicted	Actual
Berk (B)	6.74	6.55	.799	.778
York (Y)	8.19	8.14	.879	.873
F3	8.63	8.90	.920	.934
B X Y	9.58	8.42	.954	.895
Y X B	7.55	7.94	.858	.877
B X F3	8.81	9.25	.912	.956
F3 X B	7.11	7.00	.840	.845
Y X F3	8.51	8.79	.904	.924
F3 X Y	8.85	9.00	.928	.943
B X F1	9.46	8.47	.948	.892
B{F3 X Y}	9.52	9.32	.951	.933
Y X F1	9.16	9.03	.940	.931
Y{B X F3}	8.35	7.95	.899	.875
F3 X F1	9.28	10.38	.956	1.002
F2	9.24	8.27	.967	.891
Chi square	25.11		23.51	

<sup>1</sup> Breed pertains to breed of litter

TABLE A8. PREDICTED BREED MEANS, ACTUAL BREED MEANS, AND CHI SQUARE GOODNESS OF FIT TEST USING THE ADDITIVE-DOMINANCE MODEL

Mean piglet birth weight (kg) unadjusted for  
number piglets born alive per litter

Breed <sup>1</sup>	Nontransformed means		Transformed means (log 10)	
	Predicted	Actual	Predicted	Actual
Berk (B)	1.384	1.429	.141	.150
York (Y)	1.213	1.210	.073	.072
F3	1.347	1.292	.132	.106
B X Y	1.259	1.275	.099	.103
Y X B	1.428	1.495	.158	.169
B X F3	1.331	1.279	.121	.104
F3 X B	1.422	1.501	.163	.173
Y X F3	1.331	1.264	.116	.097
F3 X Y	1.252	1.356	.100	.129
B X F1	1.342	1.347	.122	.154
B{F3 X Y}	1.300	1.303	.110	.109
Y X F1	1.341	1.400	.117	.141
Y{B X F3}	1.384	1.390	.137	.137
F3 X F1	1.357	1.361	.133	.130
F2	1.372	1.471	.146	.163
Chi square	28.23		22.75	

<sup>1</sup> Breed pertains to breed of litter

TABLE A9. PREDICTED BREED MEANS, ACTUAL BREED MEANS, AND CHI SQUARE GOODNESS OF FIT TEST USING THE ADDITIVE-DOMINANCE MODEL

Mean piglet birth weight (kg) adjusted for  
number piglets born alive per litter

Breed <sup>1</sup>	Nontransformed means		Transformed means (log 10)	
	Predicted	Actual <sup>2</sup>	Predicted	Actual <sup>2</sup>
Berk (B)	1.297	1.333	.122	.115
York (Y)	1.239	1.233	.079	.077
F3	1.357	1.315	.132	.116
B X Y	1.293	1.293	.112	.108
Y X B	1.343	1.464	.134	.161
B X F3	1.340	1.326	.125	.123
F3 X B	1.339	1.375	.134	.137
Y X F3	1.336	1.254	.119	.097
F3 X Y	1.285	1.399	.106	.145
B X F1	1.385	1.335	.137	.146
B{F3 X Y}	1.339	1.360	.125	.125
Y X F1	1.381	1.440	.132	.155
Y{B X F3}	1.362	1.364	.133	.129
F3 X F1	1.402	1.429	.145	.151
F2	1.421	1.454	.156	.155
Chi square	22.24		17.35	

<sup>1</sup> Breed pertains to breed of litter

<sup>2</sup> After adjustment for litter size

TABLE A10. PREDICTED BREED MEANS, ACTUAL BREED MEANS, AND CHI SQUARE GOODNESS OF FIT TEST USING THE ADDITIVE-DOMINANCE MODEL

Breed <sup>1</sup>	Nontransformed means		Transformed means (log 10)	
	Predicted	Actual <sup>2</sup>	Predicted	Actual <sup>2</sup>
Berk (B)	16.13	16.57	1.193	1.191
York (Y)	13.40	13.45	1.098	1.097
F3	13.58	12.80	1.122	1.093
B x Y	13.41	15.43	1.116	1.176
Y x B	15.65	16.20	1.154	1.199
B x F3	14.30	15.61	1.151	1.188
F3 x B	15.30	15.29	1.159	1.171
Y x F3	14.06	14.36	1.122	1.125
F3 x Y	12.81	13.30	1.092	1.106
B x F1	13.83	13.34	1.148	1.147
B{F3 x Y}	13.62	12.73	1.132	1.091
Y x F1	13.59	14.28	1.119	1.139
Y{B x F3}	14.62	13.60	1.137	1.095
F3 x F1	13.11	15.37	1.119	1.165
F2	12.52	13.01	1.104	1.099
Chi square	34.77		32.51	

<sup>1</sup> Breed pertains to breed of litter

<sup>2</sup> After adjustment for litter size

TABLE A11. ESTIMATES OF THE MEAN, ADDITIVE, DOMINANCE, EPISTATIC EFFECTS AND STANDARD ERRORS FITTING A TWO-LOCUS INTERACTION MODEL

Parameter	Nontransformed <sup>1</sup>		Transformed (log 10)	
	Estimate	SE <sup>1</sup>	Estimate	SE <sup>1</sup>
Mean	17.35	2.40	1.375	.139
Maternal additive	1.36	0.29	0.067	.017
Litter additive	0.04	0.38	0.003	.023
Dominance				
Paternal	-3.38	1.18	-0.185	.064
Maternal	-0.40	4.49	-0.052	.277
Litter	-12.28	4.28	-0.568	.227
Maternal epistasis				
Additive X additive	1.91	1.94	0.035	.112
Additive X dominance	0.54	1.46	0.058	.089
Dominance X dominance	1.16	2.92	0.069	.181
Litter epistasis				
Additive X additive	-8.59	3.02	-0.478	.160
Additive X dominance	0.43	0.95	0.023	.053
Dominance X dominance	4.84	2.01	0.143	.114

<sup>1</sup> Standard Error

TABLE A12. ESTIMATES OF THE MEAN, ADDITIVE, DOMINANCE, EPISTATIC EFFECTS  
AND STANDARD ERRORS FITTING A TWO-LOCUS INTERACTION MODEL

Parameter	Nontransformed <sup>1</sup>		Transformed (log 10)	
	Estimate	SE <sup>1</sup>	Estimate	SE <sup>1</sup>
Mean	14.97	2.27	1.343	.152
Maternal additive	0.82	0.29	0.039	.019
Litter additive	-0.03	0.36	0.008	.025
Dominance				
Paternal	-2.92	1.02	-0.187	.061
Maternal	-3.18	4.65	-0.180	.333
Litter	-7.81	4.19	-0.511	.254
Maternal epistasis				
Additive X additive	-0.26	2.00	0.024	.135
Additive X dominance	0.89	1.48	0.038	.106
Dominance X dominance	2.90	2.99	0.161	.216
Litter epistasis				
Additive X additive	-7.37	2.86	-0.541	.169
Additive X dominance	-0.26	0.88	-0.011	.059
Dominance X dominance	1.61	1.90	0.039	.126

<sup>1</sup> Standard Error

TABLE A13. ESTIMATES OF THE MEAN, ADDITIVE, DOMINANCE, EPISTATIC EFFECTS AND STANDARD ERRORS FITTING A TWO-LOCUS INTERACTION MODEL

Mean piglet birth weight (kg) unadjusted for  
number of piglets born alive per litter

Parameter -----	Nontransformed <sup>1</sup>		Transformed (log 10)	
	Estimate	SE <sup>1</sup>	Estimate	SE <sup>1</sup>
-----	-----	-----	-----	-----
Mean	.715	.217	-.098	.067
Maternal additive	-.080	.040	.029	.009
Litter additive	-.027	.046	-.068	.011
Dominance				
Paternal	.227	.104	.054	.029
Maternal	.508	.424	.174	.119
Litter	.701	.383	.278	.127
Maternal epistasis				
Additive X additive	.248	.123	.076	.052
Additive X dominance	-.013	.142	-.122	.040
Dominance X dominance	-.248	.277	-.069	.078
Litter epistasis				
Additive X additive	.362	.256	.132	.079
Additive X dominance	.033	.104	.078	.033
Dominance X dominance	-.298	.216	-.151	.073

<sup>1</sup> Standard Error

TABLE A14. ESTIMATES OF THE MEAN, ADDITIVE, DOMINANCE, EPISTATIC EFFECTS AND STANDARD ERRORS FITTING A TWO-LOCUS INTERACTION MODEL

Parameter	Nontransformed <sup>1</sup>		Transformed (log 10)	
	Estimate	SE <sup>1</sup>	Estimate	SE <sup>1</sup>
Mean	.973	.217	.036	.067
Maternal additive	-.032	.040	-.016	.009
Litter additive	-.018	.046	-.004	.011
Dominance				
Paternal	.053	.104	.006	.029
Maternal	.549	.425	.042	.119
Litter	.332	.384	.163	.127
Maternal epistasis				
Additive X additive	.306	.123	.059	.052
Additive X dominance	.107	.142	.026	.040
Dominance X dominance	-.217	.277	.023	.078
Litter epistasis				
Additive X additive	.004	.256	.002	.079
Additive X dominance	.090	.104	.008	.033
Dominance X dominance	-.279	.216	-.129	.073

<sup>1</sup> Standard Error

TABLE A15. ESTIMATES OF THE MEAN, ADDITIVE, DOMINANCE, EPISTATIC EFFECTS AND STANDARD ERRORS FITTING A TWO-LOCUS INTERACTION MODEL

Parameter	Nontransformed <sup>1</sup>		Transformed (log 10)	
	Estimate	SE <sup>1</sup>	Estimate	SE <sup>1</sup>
Mean	18.55	3.37	1.397	.119
Maternal additive	-0.49	0.45	-0.006	.016
Litter additive	-1.07	0.70	-0.041	.020
Dominance				
Paternal	-0.77	1.60	-0.089	.051
Maternal	-18.62	6.33	-0.820	.214
Litter	2.44	7.13	0.046	.221
Maternal epistasis				
Additive X additive	-5.26	3.00	-0.216	.299
Additive X dominance	-1.39	2.04	-0.070	.071
Dominance X dominance	13.21	4.02	0.597	.138
Litter epistasis				
Additive X additive	1.71	4.63	-0.037	.144
Additive X dominance	0.59	1.78	-0.046	.054
Dominance X dominance	1.60	3.66	-0.039	.117

<sup>1</sup> Standard Error

TABLE A16. PREDICTED BREED MEANS, ACTUAL BREED MEANS, AND CHI SQUARE GOODNESS OF FIT TEST USING A TWO-LOCUS INTERACTION MODEL

Breed <sup>1</sup>	Number piglets born alive per litter		Number piglets born alive per litter	
	Nontransformed means Predicted	Actual	Transformed means (log 10) Predicted	Actual
Berk (B)	9.27	7.90	0.862	0.862
York (Y)	12.07	10.70	1.002	1.002
F3	10.82	10.71	1.025	1.020
B X Y	13.71	10.58	1.051	1.001
Y X B	10.45	9.44	0.917	0.956
B X F3	10.23	10.25	0.991	0.980
F3 X B	9.00	7.20	0.875	0.857
Y X F3	10.48	9.93	1.006	0.984
F3 X Y	11.98	11.17	1.023	1.042
B X F1	10.90	9.87	1.017	0.956
B{F3 X Y}	11.61	11.50	1.042	1.042
Y X F1	11.15	11.10	1.031	1.033
Y{B X F3}	10.16	9.55	0.956	0.956
F3 X F1	11.49	11.75	1.051	1.060
F2	9.80	9.76	0.958	0.958
Chi square	> 50		7.73	

<sup>1</sup> Breed pertains to breed of litter

TABLE A17. PREDICTED BREED MEANS, ACTUAL BREED MEANS, AND CHI SQUARE GOODNESS OF FIT TEST USING A TWO-LOCUS INTERACTION MODEL

Breed <sup>1</sup>	Number piglets weaned per litter		Transformed means (log 10)	
	Nontransformed means Predicted	Actual	Predicted	Actual
Berk (B)	6.55	6.55	.778	.778
York (Y)	8.14	8.14	.873	.873
F3	9.15	8.90	.954	.934
B X Y	9.34	8.42	.934	.895
Y X B	7.70	7.94	.856	.877
B X F3	8.84	9.25	.911	.956
F3 X B	7.17	7.00	.852	.845
Y X F3	8.69	8.79	.914	.924
F3 X Y	8.85	9.00	.933	.943
B X F1	9.43	8.47	.941	.892
B{F3 X Y}	9.32	9.32	.933	.933
Y X F1	9.27	9.03	.944	.931
Y{B X F3}	7.94	7.95	.875	.875
F3 X F1	9.73	10.38	.984	1.002
F2	8.27	8.27	.891	.891
Chi square	10.02		6.12	

<sup>1</sup> Breed pertains to breed of litter

TABLE A18. PREDICTED BREED MEANS, ACTUAL BREED MEANS, AND CHI SQUARE GOODNESS OF FIT TEST USING A TWO-LOCUS INTERACTION MODEL

Mean piglet birth weight (kg) unadjusted for  
number piglets born alive per litter

Breed <sup>1</sup>	Nontransformed means		Transformed means (log 10)	
	Predicted	Actual	Predicted	Actual
Berk (B)	1.432	1.429	.150	.150
York (Y)	1.218	1.210	.072	.072
F3	1.297	1.292	.101	.106
B X Y	1.286	1.275	.134	.103
Y X B	1.446	1.495	.076	.169
B X F3	1.279	1.279	.121	.104
F3 X B	1.528	1.501	.125	.173
Y X F3	1.268	1.264	.092	.097
F3 X Y	1.358	1.356	.154	.129
B X F1	1.347	1.347	.156	.154
B{F3 X Y}	1.307	1.303	.109	.109
Y X F1	1.336	1.400	.128	.141
Y{B X F3}	1.392	1.390	.137	.137
F3 X F1	1.365	1.361	.136	.130
F2	1.478	1.471	.163	.163
Chi square	4.48		43.25	

<sup>1</sup> Breed pertains to breed of litter

TABLE A19. PREDICTED BREED MEANS, ACTUAL BREED MEANS, AND CHI SQUARE GOODNESS OF FIT TEST USING A TWO-LOCUS INTERACTION MODEL

Mean piglet birth weight (kg) adjusted for  
number piglets born alive per litter

Breed <sup>1</sup>	Nontransformed means		Transformed means (log 10)	
	Predicted	Actual <sup>2</sup>	Predicted	Actual <sup>2</sup>
Berk (B)	1.333	1.333	.115	.115
York (Y)	1.233	1.233	.077	.077
F3	1.316	1.315	.115	.116
B X Y	1.299	1.293	.113	.108
Y X B	1.364	1.464	.144	.161
B X F3	1.277	1.326	.112	.123
F3 X B	1.421	1.375	.162	.137
Y X F3	1.304	1.254	.112	.097
F3 X Y	1.384	1.399	.132	.145
B X F1	1.389	1.335	.150	.146
B{F3 X Y}	1.360	1.360	.125	.125
Y X F1	1.416	1.440	.150	.155
Y{B X F3}	1.364	1.364	.129	.129
F3 X F1	1.428	1.429	.153	.151
F2	1.454	1.454	.155	.155
Chi square	5.59		4.83	

<sup>1</sup> Breed pertains to breed of litter

<sup>2</sup> After adjustment for litter size

TABLE A20. PREDICTED BREED MEANS, ACTUAL BREED MEANS, AND CHI SQUARE GOODNESS OF FIT TEST USING A TWO LOCUS INTERACTION MODEL

Breed <sup>1</sup>	Nontransformed means		Transformed means (log 10)	
	Predicted	Actual <sup>2</sup>	Predicted	Actual <sup>2</sup>
Berk (B)	16.56	16.57	1.191	1.191
York (Y)	13.45	13.45	1.097	1.097
F3	13.78	12.80	1.105	1.093
B X Y	16.48	15.43	1.182	1.176
Y X B	17.82	16.20	1.195	1.199
B X F3	14.98	15.61	1.172	1.188
F3 X B	15.83	15.29	1.179	1.171
Y X F3	14.20	14.36	1.109	1.125
F3 X Y	14.08	13.30	1.103	1.106
B X F1	15.57	13.34	1.211	1.147
B{F3 X Y}	13.63	12.73	1.091	1.091
Y X F1	14.80	14.28	1.147	1.139
Y{B X F3}	14.50	13.60	1.095	1.095
F3 X F1	14.37	15.37	1.143	1.165
F2	13.99	13.01	1.099	1.099
Chi square	45.91		5.07	

<sup>1</sup> Breed pertains to breed of litter

<sup>2</sup> After adjustment for litter size