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Estimation of variance components including competitive effects of Large White growing gilts¹

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ABSTRACT: Records of on-test ADG of Large White gilts were analyzed to estimate variance components of direct and associative genetic effects. Models included the effects of contemporary group (farm-barn-batch), birth litter, pen group, and direct and associative additive genetic effects. The area of each pen was 14 m². The additive genetic variance was a function of the number of competitors in a group, the additive relationships between the animal performing the record and its pen mates, and the additive relationships between pen mates. To partially account for differences in the number of pen mates, a covariable ($q_i = 1, 1/n,$ or $1/n^{1/2}$) was added to the associative genetic effect. There were 4,946 records from 2,409 litters and 362 pen groups. Pen group size ranged from 12 to 16 gilts. Analyses by REML converged very slowly. A grid search

showed that the likelihood function was almost flat when the additive genetic associative effect was fitted. Estimates of direct and associative heritability were 0.15 and 0.03, respectively. Within the BLUPF90 family of programs, the mixed-model equations can be set up directly. For variance component estimation, simple programs (REMLF90 and GIBBSF90) worked without modifications, but more optimized programs did not. Estimates obtained using the three values of q_i were similar. With the data structure available for this study and under an environment with relative low competition among animals, accurate estimation of associative genetic effects was not possible. Estimation of competitive effects with large pen size is difficult. The magnitude of competition effects may be larger in commercial populations, where housing is denser and food is limited.

Key Words: Competition, Genetic Effects, Growth, Swine

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Introduction

If penned animals are evaluated for individual performance, more dominant animals may be selected. If such animals have a negative effect on the performance of their peers, performance of the pen may decrease below the sum of the direct genetic potential of individual pen members. To achieve improved group performance, animals should be selected not only for faster growth but also for less competition (Muir and Schinckel, 2002).

One possibility for such selection is group selection, which comes at a cost of a rapid increase in inbreeding

(Muir and Craig, 1998). Muir and Schinckel (2002) presented an alternative approach by including in the model the direct effect of the animal and also competitive effects of all pen mates. Muir (2005) extended the model to include associative effects in breeding programs for forest trees and animals. Van Vleck and Casady (2005) investigated the competitive model using simulation; they recovered the original parameters of the model, although they also reported some unexpected results.

In swine breeding, rate of genetic progress at the nucleus level is high, but progress is much smaller or nonexistent at the commercial level. Stocking rates in commercial finisher barns are usually greater, leading to some feed limitation. Both conditions likely increase competition. Lutaaya et al. (2001) studied joint evaluation of purebreds and crossbreds in swine, and estimated genetic correlations between two purebred lines and their reciprocal F₁ terminal crosses. Those correlations were smaller for depth of backfat (0.32 and 0.70) than for lifetime daily gain (0.99 and 0.62). Different management (i.e., feeding environments) for purebreds and for crossbreds might result in backfat operating as

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Table 1. Number of records, unadjusted means, and standard deviations for traits of Large White gilts

Item	No.	Mean	SD
Final BW, kg	4,946	120	9.5
ADG, g	4,946	611	46.0
Pen size	12 to 16	13.7	1.31
Animals without records	3,058		
Total animals	8,004		

a different trait at multiplication vs. commercial levels, which could be explained partially by greater competition among animals in commercial operations. The purpose of this study was to apply the competition model to a population of swine for growth during test.

Materials and Methods

Data

Field data were provided by the Smithfield Premium Genetics Group (Roanoke Rapids, NC) from pure-line Large White gilts. Test performance was measured with an off-test target age of 160 d. Traits included off-test weight and age. Growth was expressed as days to reach 113.5 kg as determined by NSIF (1997) and ADG (g/d). Tests were performed in standard confinement facilities. Gilts were housed in mechanically ventilated barns with concrete slatted flooring. A standard corn-soy based diet was provided ad libitum, and was prepared to meet the growing phase nutrient requirements.

The original data comprised 6,957 records spanning 4 yr (2001 to 2004). Records within an acceptable range for off-test age (115 to 210 d) and weight (54.4 to 158.7 kg) were kept for analyses. In addition, records from smaller pen groups (<12) were discarded. Contemporary groups were defined for animals managed together as farm-barn-batch. Each individual was assigned to a specific pen group within a barn and on test date. After edits, there were 4,946 test performance records from 2,409 litters (Table 1), with 88 contemporary groups and 362 pen groups. The area of each pen was 14 m². The pedigree file had a total of 8,004 animals. The nature of the test data, in which only part of the female sibs from each litter were tested, imposed a limitation on the additive relationships within pen. There were, on average, 1.2 and 2.6 full and half sibs per pen, respectively.

Models and Analyses

A set of preliminary analyses for the primary growth trait (ADG) were carried out to test models differing in number of fixed and random factors (Table 2). In particular, there was interest in evaluating the effects of contemporary group, pen, and litter of birth. The only previous modeling report for competition effects

in livestock was by Van Vleck and Cassady (2005), who simulated data similar to that occurring in swine production. Their data were simulated with the overall mean as the fixed effect, and with a constant pen size of six. In their analyses, pen was treated as a fixed factor, as a random factor, or ignored. In practice, pen groups are larger and unequal, and contemporary effects exist. Here, pen group size varied within a range of 12 to 16 (averaging 13.7) animals, which is smaller than what is commonly found commercially. The general model for analysis for ADG (g/d) was as follows:

$$y_{ijklm} = cg_k + d_i + \sum c_j + pg_l + l_m + e_{ijklm} \quad [1]$$

where y_{ijklm} is the observed response for animal i in contemporary group class k , belonging to pen group l , and born in litter m ; d is the direct additive genetic effect of animal i ; c is the competition or associative additive genetic effects summed over the j pen mates ($j = 11$ to 15) of animal i ; and e_{ijklm} is the residual variance. All associative effects in one equation point to the same area in the mixed-model equations. In a linear mixed model with the matrix of additive relationship among animals (A), and including birth litter and pen group as uncorrelated random factors, the variances of the random factors are as follows:

$$\text{Var} \begin{bmatrix} d \\ c \\ pg \\ l \\ e \end{bmatrix} = \begin{bmatrix} A\sigma_d^2 & A\sigma_{dc} & 0 & 0 & 0 \\ A\sigma_{dc} & A\sigma_c^2 & 0 & 0 & 0 \\ 0 & 0 & I\sigma_{pg}^2 & 0 & 0 \\ 0 & 0 & 0 & I\sigma_l^2 & 0 \\ 0 & 0 & 0 & 0 & I\sigma_e^2 \end{bmatrix}$$

The matrix A links direct and associative genetic effects through a relationship within and across pens. The contribution of the additive genetic variance to the total phenotypic variance

$$V(g_i) = V \left(d_i + \sum_{j=1}^n c_j \right)$$

depends on the number of competitors, the additive relationship between the animal with the record and its pen mates (a_{ij}), and the additive relationship between pen mates ($a_{j'j''}$). Assuming a constant additive relationship ($a_{ij} = a_{j'j''}$) among members of a pen:

$$V(g_i) = \sigma_d^2 + n\sigma_c^2 + n(n-1)a_{j'j''}\sigma_c^2 + 2na_{ij}\sigma_{dc} \quad [2]$$

Equation [2] can be presented for several cases.

Case 1) Competitors are litter mates:

$$\begin{aligned} V(g_i) &= V(d_i) + V \left(\sum_{j=1}^n c_j \right) \\ &= \sigma_d^2 + n\sigma_c^2 + n(n-1)0.50\sigma_c^2 + 2n0.50\sigma_{dc} \\ &= \sigma_d^2 + \left[n + \frac{n(n-1)}{2} \right] \sigma_c^2 + n\sigma_{dc} \end{aligned}$$

Table 2. Models compared for average daily gain of Large White gilts considering direct and associative additive genetic effects^a

Model	Fixed effect	Random effect				
		Litter	Pen	Animal additive genetic		Residual
				Direct	Associative	
1	CG	X	—	X	—	X
2	Pen ^b	X	—	X	—	X
3	CG	—	X	X	—	X
4	CG	X	X	X	—	X
5	CG	X	X	X	X	X

^aCG = contemporary group. “X” indicates that the effect was included in the model.

^bPen = pen-weight date group.

Case 2) Competitors are paternal half-sibs:

$$\begin{aligned}
 V(g_i) &= V(d_i) + V\left(\sum_{j=1}^n c_j\right) \\
 &= \sigma_d^2 + n\sigma_c^2 + n(n-1)0.25\sigma_c^2 + 2n0.25\sigma_{dc} \\
 &= \sigma_d^2 + \left[n + \frac{n(n-1)}{4}\right]\sigma_c^2 + \frac{n}{2}\sigma_{dc}
 \end{aligned}$$

Case 3) Competitors are not related:

$$\begin{aligned}
 V(g_i) &= V(d_i) + V\left(\sum_{j=1}^n c_j\right) \\
 &= \sigma_d^2 + n\sigma_c^2
 \end{aligned}$$

The relationship matrix accounts for differences in relationships among members of the pen groups; however, the genetic (co)variance structure varies with the additive relationship between pen mates, and with their number. Accounting for differences in the number of competitors within and across pens for a general case is complicated. These differences can be partially accounted by adding a covariable to the associative genetic effect, which is analogous to the classic random regression model:

$$\dots d_i + \sum_{j=1}^n c_j \dots \Rightarrow \dots d_i + q_i \sum_{j=1}^n c_j \dots$$

The value of $q_i = 1$ corresponds to the model as initially described by Muir and Schinckel (2002). Values other than one can be used for q_i . A value of $q_i = 1/n$ decreases the changes in variance due to differences in relationship among competitors in Cases 1 and 2. In one extreme, if the relationship is ignored or if it is close to zero, $V(g_i) = \sigma_d^2 + 1/n \sigma_c^2$. In the other extreme, if the relationship is one (i.e., pen mates are clones), $V(g_i) = \sigma_d^2 + \sigma_c^2 + 2\sigma_{dc}$. For intermediate values of the relationship between pen mates, it works as a weighting factor for the associative genetic variance between $1/n$ and 1. A value of $q_i = 1/n^{1/2}$ stabilizes the variance in

Case 3. In comparisons, estimates obtained using the three values of q_i were similar. Estimates reported in this article are for $q_i = 1/n$. When all pens have equal numbers of pigs, q_i is simply a scale factor, and results are equivalent. Differences among models with different q_i probably are small when variations in pen size are small.

Analyses were done by REML methods using programs of the BLUPF90 family (BGF90) (Misztal et al., 2002). An example of the parameter file to implement the analysis is provided in Appendix A.

Results and Discussion

Table 1 shows basic statistics for the performance data while on test. Gilts ended test averaging 120 kg BW, and their ADG was on average 611 g/d.

Estimates of variance components for ADG using different models (Table 2) are presented in Table 3. Analysis excluding the pen effect (Model 1) inflated the residual variance. Ignoring litter effect but defining pen as random effect (Model 3) led to a larger estimate of the direct additive genetic variance, which was of a magnitude similar to the sum of the litter plus the additive variance in the model including both (Models 1 and 2). Consequently, a larger estimate of heritability (0.26) was obtained when the random litter effect was ignored than when such an effect was accounted for in the model (0.16). On the basis of a likelihood ratio test, a model including contemporary group as a fixed effect and random effects of litter and pen (Model 4) was significantly better than models with either random effect separately (Models 1 and 3). Thus, estimates of variance components from Model 4 were used for comparison with corresponding estimates with Model 5, which included the associative additive genetic effects.

When associative genetic effects were included (Model 5; Table 3), the convergence rate was slow and sensitive to the choice of starting values. Convergence to a false local maximum occurred when the analysis was initiated with different starting values. The estimate for the associative genetic variance was found to correspond to spurious convergence. Slow progress was due in part to many nonzero coefficients in the design

Table 3. Estimates of variance components for average daily gain of Large White gilts considering direct and associative additive genetic effects

Model	-2 log likelihood	Estimates of variance components, g ² /d ²					Heritability	
		Litter	Pen ^a	Additive genetic			Direct	Associative
				Direct	Associative	Residual		
1	50,099.1	176	—	271	—	1,290	0.16	—
2	47,672.8	166	—	259	—	1,230	0.16	—
3	50,065.8	—	101	462	—	1,240	0.26	—
4	50,038.0	167	99	266	—	1,225	0.15	—
5 ^b	50,037.9	168	90	265	50	1,224	0.15	0.03

^aPen = pen-weight date group.

^bNo covariance between direct and associative additive genetic effects.

matrix for the associative effect, with each record having contributions for all pen group mates instead of just one coefficient for the direct additive genetic effect. To see whether convergence was to a global or local maximum, a grid search was implemented for estimates of the associative genetic variance that maximized the likelihood function. For this search, only the direct and associative variances were included (i.e., no covariance between them); variances for litter, pen and residual effects were held constant as shown for Model 5 (Table 3). Results from the grid search are presented in Table 4. The likelihood was almost flat, indicating insufficient information to estimate the variance of the associative effect, and dubious convergence. A large standard error would be expected for such a variance estimate. In addition, a decrease in pen variance was observed when associative genetic variance was fitted in the model, as expected, but it was only approximately 10% compared with the model excluding that effect (Models 3 and 4 vs. Model 5). Similar results were obtained regardless of the choice of adjustment factor for pen size (i.e., 1, 1/n, or 1/n^{1/2}).

Problems with estimation of associative genetic effects in this study could be due to several reasons. The stocking rate did not encourage competition, so there was not much incentive to express antagonism. A regression analysis of performance on pen size was not significant, indicating that the overall pen mean was not affected by the number of animals interacting in a pen within the range used in the present study. There might be more competition in typical commercial finishing operations, where stocking density is allocated

to maximize throughput, which might lead to more antagonistic interactions for resources, especially space and food. The additive relationships present among pen mates and across pens also may be insufficient to allow separation of direct from associative additive genetic variance. In this study, only part of each full-sib family was tested (i.e., on average, only one to two littermate gilts were present in each pen). There were, on average, only 9% littermates and 19% paternal half-sib gilts within a pen. Therefore, ignoring other sources of relationship, the average within-pen relationship was close to 10%. Finally, when the number of competing animals in a pen is large, separation of dominant from passive animals may be difficult. In a model with multiple sires in a pasture that is similar to the competitive model, identifying sires was not very successful (van Kaam et al., 2003). Thus, computations with large pen sizes may be difficult.

Software Considerations

Analysis with the competitive model requires software that can accommodate a variable number of competitor effects, all contributing to the same block of equations, with possible variable weights for these effects if the number of competitors is variable. A variable number of competitors can be implemented by defining the maximum number of competitors and supporting the missing effects. Variable weights can be supported through random regression. Making all competitor effects contribute to the same block of equations can be implemented by setting the number of levels for all competitor effects except the last one to zero. The last competitor effect has the actual number of levels, which is equal to the number of animals (Appendix A). For variance component estimation, the software needs to estimate (co)variances for only one competitor effect, even though many are defined. Within the BLUPF90 family of programs (Misztal et al., 2002), the mixed-model equations can be set up directly without any modifications to the programs, as outlined in Appendix A. For more optimized programs (AIREMLF90 and GIBBS2F90), modifications are needed because these programs calculate variance components for every ran-

Table 4. Estimates of -2 log likelihood (plus 50,037) at selected direct and associative genetic variances (grid search) for average daily gain of Large White gilts

Additive associative genetic variance, g ² /d ²	Additive direct genetic variance, g ² /d ²		
	260	265	270
30	0.982	0.952	0.951
50	0.974	0.946	0.948
70	0.982	0.957	0.962

dom effect in the model. Thus, they estimate variances for many associative effects instead of only one.

Implications

Successful parameter estimation for a competition model requires that several conditions be fulfilled. First, the environment of the animals should encourage expression of competition. Second, the average group size needs to be small. Results suggest that animals within and across pens need to be sufficiently related. Many problems with the competitive model still need to be addressed. One problem is stabilization of animal variances with changing numbers of competitors. An important problem is whether prediction of performance with one pen size and a specific environment is meaningful for prediction with a different pen size and a different environment. Lastly, mortality as a result of competition may have an important effect on the results of analysis including associative effects, and it will be considered in future research.

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Appendix

Shown below is an example of the parameter file used to implement an analysis with BLUPF90 and related programs (BGF90), including direct and associative additive genetic effects with an assumed maximum pen size 16. Additional instructions are available in the distribution Website: <http://nce.ads.uga.edu/~ignacy/newprograms.html>.

Name of pedigree file: ped

Name of data file: dd

Data file structure

1. Contemporary group
2. Pen group
3. litter of birth
4. Animal
5. Competitor 1
6. Competitor 2 (0 if missing)
7. ...
19. Competitor 15 (0 if missing)
20. Nested covariable ($q_i = 1, 1/[\text{pen size} - 1]$ or $1/[\text{pen size} - 1]^{1/2}$)
21. Gain

BLUPF90 parameter file created by RENF90

DATAFILE

dd

NUMBER_OF_TRAITS

1

NUMBER_OF_EFFECTS

19

OBSERVATION(S)

21 # average daily gain (g)

WEIGHT(S)

```

EFFECTS: POSITIONS_IN_DATAFILE NUMBER_OF_LEVELS TYPE_OF_EFFECT [EFFECT NESTED]
  1   88  cross # contemporary group
  2  362  cross # pen group
  3 2409  cross # litter
  4 8004  cross # Animal
20   0   cov 5 # pen mate number 1
20   0   cov 6 # pen mate number 2
20   0   cov 7 # pen mate number 3
20   0   cov 8 # pen mate number 4
20   0   cov 9 # pen mate number 5
20   0   cov 10 # pen mate number 6
20   0   cov 11 # pen mate number 7
20   0   cov 12 # pen mate number 8
20   0   cov 13 # pen mate number 9
20   0   cov 14 # pen mate number 10
20   0   cov 15 # pen mate number 11
20   0   cov 16 # pen mate number 12
20   0   cov 17 # pen mate number 13
20   0   cov 18 # pen mate number 14
20 8004  cov 19 # pen mate number 15
RANDOM_RESIDUAL VALUES
1224.
RANDOM_GROUP
  4 5      # direct and associative animal effects
RANDOM_TYPE
add_animal
FILE
ped
(CO)VARIANCES
 265.  0
  0  50.
RANDOM_GROUP
  2      # effect 2 (pen) as uncorrelated random factor
RANDOM_TYPE
diagonal
FILE

(CO)VARIANCES
 90.
RANDOM_GROUP
  3      # effect 3 (litter) as uncorrelated random factor
RANDOM_TYPE
diagonal
FILE

(CO)VARIANCES
168.

```

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