

Group Selection in Swine – A Case Study

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The Problem

Our goal is to improve the performance of animals – we try to map this performance into a single dimension, a measure of economic value. This was initially proposed by Hazel (1943) when the concept of a selection index was presented. The selection index provides a simple way to weight the value of genetic change realized in any given trait with the other traits that were of interest and combine them so that the index optimized the genetic change in terms of economic return.

New technologies have become available that increase the accuracy in which estimated breeding values are calculated, facilitating increasingly complex selection programs and the ability to approach the theoretical limits of predicted genetic change. Swine has offered a simple system to transfer this genetic change to the end user by using a traditional pyramid system that allowed the multiplication of the animals selected at the pinnacle of the system and then used at the multiplication level and finally the end user gained the value when terminal animals were produced.

The problem was that this system did not seem to work as well in practice as it did in theory. Genetic trends within the nucleus or elite levels were variable, but generally in the direction that was predicted (Figure 1). Regression equations could be fit through the predicted breeding values against time and the lines were in the appropriate direction. But, the rate of change realized by the end user at the enterprise level did not seem to parallel the nucleus and multiplication tiers of the traditional genetic pyramid. Even though breeding values appeared to be moving in the desired direction at the nucleus level, phenotypic trends may not be changing as desired (Figure 2).

Perhaps this was a unique occurrence to Newsham Hybrids (USA) – perhaps we were the only breeding organization where this was happening. But, it did raise the question within in Newsham Hybrids organization - why this was happening and what could be done to increase the performance at the enterprise level so that it followed accepted selection theory?

A Possible Reason for the Problem

The fundamental theory of selection involves the very simple concept of –

$$p_i = g_i + e_i,$$

Where p_i = phenotype of the i th individual,
 g_i = genotype of the i th individual, and
 e_i = random environment of the i th individual.

Selection is based on the premise that individuals with superior g_i values can be identified and retained for the next generation. Technologies by which we estimate this genetic component and the relationship between the genotype and phenotype have been the foundation which we have built breeding and selection programs. Theoretical ways of partitioning out non-additive, epistatic, common environmental and maternal effects have been developed to provide more accurate estimates of the additive genetic value of an individual.

Griffing (1967,1968a, 1968b,1969, 1976a and 1976b) in a series of papers proposed that if there is competition amongst individuals within a test group, the actual genetic change may not be as predicted. In his 1967 paper he states,

... the usual gene model for a given genotype must be extended to include not only direct effects of its own genes, but also associated contributions from other genotypes in the group ...

Griffing (1967) proposed that genetic change for random groups of size n can be presented as –

$$\delta G = (i/\sigma) (\sigma^2_d + (n-1) {}_a\sigma_{ad}), \quad (1)$$

Where δG = Genetic change for the trait of interest
 i = Selection intensity,
 σ = Phenotypic standard deviation,
 σ^2_d = direct additive genetic variance,
 ${}_a\sigma_{ad}$ = additive covariance between the direct genetic component and the associative effect (competition).

Griffing points out in this paper that if *direct and associate effects for most genes are negatively related the covariance term, ${}_a\sigma_{ad}$, can be negative*. So, it is apparent that if ${}_a\sigma_{ad}$ is less than zero and the group size is relatively large and the absolute value of this term is greater than σ^2_d the value of δG will also be less than zero. Griffing's proposed solution to this problem is to select on groups of individuals rather than practice individual selection within groups.

If selection is based on the group as the selection unit, then for groups of size n (Muir, 2005),

$$\delta G = (1/n) \cdot (i_{gr} / \sigma_{gr}) \cdot (\sigma^2_d + 2(n-1) \cdot {}_a\sigma_{ad} + (n-1)^2 \cdot \sigma^2_a), \quad (2)$$

Where, n = size of groups,
 i_{gr} = Standardized selection differential based on the group means,
 σ_{gr} = Phenotypic standard deviation of the group mean,
 σ^2_a = Additive genetic variance for associative effects,
 $\sigma^2_d, {}_a\sigma_{ad}$ = as listed in equation 1.

Griffing's compelling argument for the negative covariance between the associative effect and the direct additive effect for the trait of interest lead Muir to investigate the use of selection on

family groups as applied to poultry (Craig and Muir, 1989, 1993). An overview of the group selection procedures developed by Muir was presented to NSIF at the 2001 meetings (Muir, 2001).

In the NSIF paper Muir provides numerous references to research that shows that use of group selection increased the performance of the populations evaluated and changed the behavior of individuals being evaluated. This paper is an excellent source of information concerning the merits of group selection.

Application of Group Selection to Swine

In 1994 Newsham Hybrids (USA) began working with Drs. Muir and Schinckel to develop a protocol that could migrate the group selection theory developed by Griffing and applied to poultry by Muir to the development of a breeding program for the improvement of swine. In 1996, Newsham Hybrids (USA) Inc. initiated a program to practice selection on groups of half sibs within their nucleus farm.

Implementation

The basic method is to rear individuals in half-sib groups and choose the best performing individuals within the group.

This statement appears in one of the documents that Newsham Hybrids (USA) developed describing how the group selection would be implemented within the nucleus breeding program. It would appear simple enough – modify a finishing facility that was designed to test 18 same sex individuals within a pen to now have half sib families within the pen. Since groups are now the experimental unit which selection is practiced – consider the impact that filling a single barn with a fixed number of pens with enough sire diversity to have some type of selection intensity. Finally, add the possible influence of possibly increasing the rate of inbreeding because families are now selected rather than individuals.

The following testing protocol was employed,

- Evaluate 300 sires per line per year,
- Each sire would produce 3-6 litters in a week,
- Six sires per line per week would be evaluated,
- If more than 3 litters were farrowed by a sire,
 - Select the best three litters using a litter index to populate the pen,
- Target 18 pigs/pen,
 - 10 gilts and 8 barrows,
 - Adjust the gilt:barrow relationship depending on available numbers, and
- Select 2 boars per litter and pen them independently.

Selection procedures,

- Groups were evaluated based on an index,
- Three of the six half sib family groups were selected,
- One boar from each of the three selected families were retained,
- Two gilts were selected from each of the top three family groups,
- Selection of individuals (boars and gilts) within each family group was based on non-performance traits (Feet, legs, structure, soundness, underlines ...), and
- Based on the size of each population, 6 gilts/week selected would result in a 70% replacement rate at the nucleus level.

The system was very complex and presented an inefficient use of gilts and boars produced by the Nucleus. The selection unit under this system is the sire. Since gilts are selected at random within the top 3 performing sire families, the selection intensity will not be greater than 50%. These two aspects of the protocol would be viewed as a negative. The potential increase in selection intensity using *traditional* selection methods and concerns about increasing the rate of inbreeding would be reason for most animal breeders to question the use of group selection. But, if the accuracy is improved and the number of families increased enough – both of these concerns may not be of importance.

Newsham Hybrids (USA) followed the group selection protocol from 1996 through 2002. In 2002, Seghers Genetics purchased Newsham Hybrids (USA) and the group selection program which was run under the name of GENTEL[®] Selection. Figure 3, presents the phenotypic trend observed at the nucleus before and after the group selection protocol was implemented. The phenotypic trend now seems to be moving in the desired direction.

Retrospective Appeal of Group Selection

The purpose of adopting a group selection protocol was to accelerate the rate of genetic response that seemed to be lost under accepted selection protocols. By selecting truly genetically superior animals the rate of genetic change should increase and the performance at the enterprise level would also increase.

After selection has occurred for multiple generations a great deal of antidotal evidence of benefits occurring from the selection program.

- Behavior within a pen appeared to be more docile
- Space allocation in the finishing phase could be reduced
- Reduction of animal loss from small pigs and death in finishing
- Increase in number of pigs marketed at full market value
- Change in behavior may have positive impact on the image of confinement production

Future of Group Selection

In 1998 a document internal to Newsham Hybrids (USA) was published that provided an extension to the traditional linear model for the prediction of breeding values to include associative effects. Figure 4, graphically shows the interaction between three pigs in a pen. The arrows that link each pig show the combination of associative effects that need to be estimated.

If we make the assumption that these associative effects have a direct additive component then we may be able to estimate that value using the appropriate mixed model. The model proposed by Muir, Schinckel, Avalos and Wang (1998) was:

$$Y = X\beta + Z_d\mu_d + Z_a\mu_a + \varepsilon \quad (3)$$

Where, Y = vector of observed phenotypes,
 $X\beta$ = known fixed effects,
 μ_d = vector of direct additive genetic effects,
 Z_d = incidence matrix corresponding to the direct effects,
 μ_a = vector of direct additive associative genetic effects
 Z_a = incidence matrix corresponding to the associative effects (identifying the animals by group).

The mixed model equations then become,

$$\begin{bmatrix} X'X & X'Z_d & X'Z_a \\ Z_dX' & Z_d'Z_d + k_1A^{-1} & Z_d'Z_a + k_2A^{-1} \\ Z_aX' & Z_a'Z_d + k_2A^{-1} & Z_a'Z_a + k_3A^{-1} \end{bmatrix} \cdot \begin{bmatrix} \beta \\ \mu_d \\ \mu_a \end{bmatrix} = \begin{bmatrix} X'Y \\ X'Z_dY \\ X'Z_aY \end{bmatrix}$$

where,

$$\begin{bmatrix} k_1 & k_2 \\ k_2 & k_3 \end{bmatrix} = \sigma_e^2 \cdot \begin{bmatrix} \sigma_{u_d}^2 & \sigma_{(u_d, u_a)} \\ \sigma_{(u_a, u_d)} & \sigma_{u_a}^2 \end{bmatrix}^{-1}$$

And $\sigma_{u_d}^2$ is the variance of the direct additive genetic effects, $\sigma_{u_a}^2$ is the variance of associative additive genetic effect and $\sigma_{(u_d, u_a)}$ is the covariance between direct additive and associative genetic effects, A^{-1} is the inverse of the numerator relationship matrix.

This system now allows a breeding value to be estimated directly for the trait of interest and for the additive genetic value for the associative effect. An index could then be developed to optimize genetic change using information from both the direct and associative effect. Muir (2005) suggests that the optimal index to predict the genetic merit of an individual is,

$$I_i = \hat{d}_i + (n-1)\hat{a}_i$$

Where I_i = Index value for the i^{th} individual,
 \hat{d}_i = Estimated direct effect for the i^{th} individual,
 n = number of pigs in a pen, and
 \hat{a}_i = Estimated associative genetic effect for the i^{th} individual.

Since Muir and Schinckel's (2002) original publication of this model to account for associative effects a number of other papers have been published that also address the issue (Van Vleck and Cassady, 2004; Van Vleck and Cassady, 2005, Arango et al, 2005; and Muir, 2005). The studies published by Van Vleck and Cassady (2004, 2005) provide excellent overviews of the protocols required to set up the necessary mixed model equations. They also investigate how the models behave under a variety of parameter sets that change the relationship between the known variance components of interest. Arango et al, 2005, applies the methods to a population of Large White gilts evaluated for average daily gain. Some of the implementation problems are presented.

The 2005 paper by Muir presents an extension of the problem to include Forest Tree breeding and also presents results from a selection study conducted using Japanese quail. This study presents results from using both the group selection using half sib families, similar to the protocol utilized by Newsham Hybrids (USA) and the mixed model solutions to develop an index that uses both the direct and associative effects compared to traditional direct selection. Results show that the greatest rate of change occurs when the mixed model methods are used to estimate breeding values, selection on family groups is less efficient than using the mixed model procedures.

Summation

Within environments where competition may exist, some method of accounting for the genetic component of competition warrants consideration. Use of family group selection is difficult to administer, but it clearly accounts for all sources of genetic input when evaluating animals. The mixed model approach will probably allow more efficient application of the group selection theory.

Work continues to determine how to make the mixed model solutions work more effectively. Currently, Van Vleck is using simulation models to investigate if there are ways to distribute genotypes both between and within pens to increase the solution efficiency of the mixed model equations. The problem of multiple trait evaluation has yet to be addressed. The accuracy of which a covariance is estimated seems to be more sensitive to data structure and design than the variance components. This may make using the associative effects more difficult to include into a multiple trait breeding program.

It should be pointed out that the Purdue University Research Foundation applied and was granted a patent (**WO 02/076190 A2**) by the *World Intellectual Property Organization* for INCORPORATION OF COMPETITIVE EFFECTS IN BREEDING PROGRAM TO INCREASE LEVELS AND IMPROVE ANIMAL WELL BEING. The inventor of the patent is listed as William M. Muir.

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Figure 1: Genetic Trend at Nucleus (EBV over time)

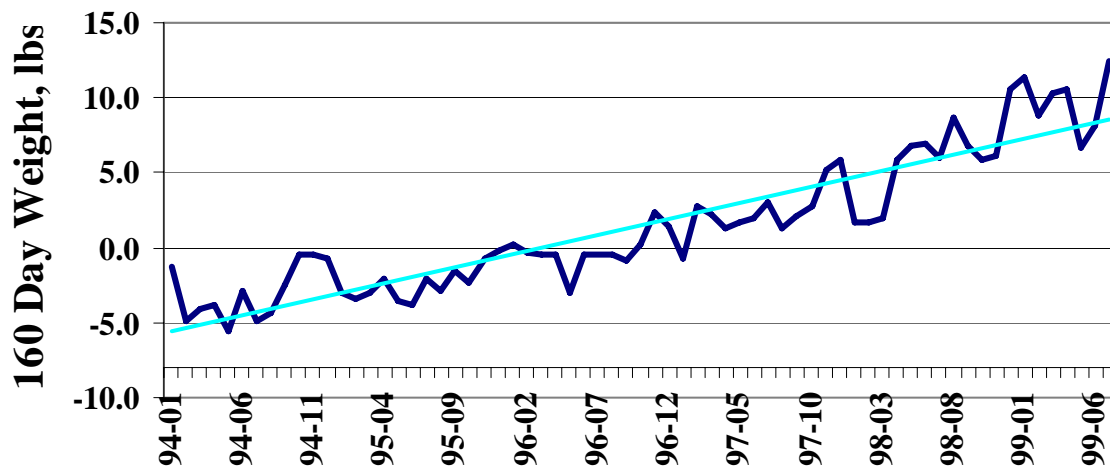


Figure 2: Phenotypic Trends at the Nucleus

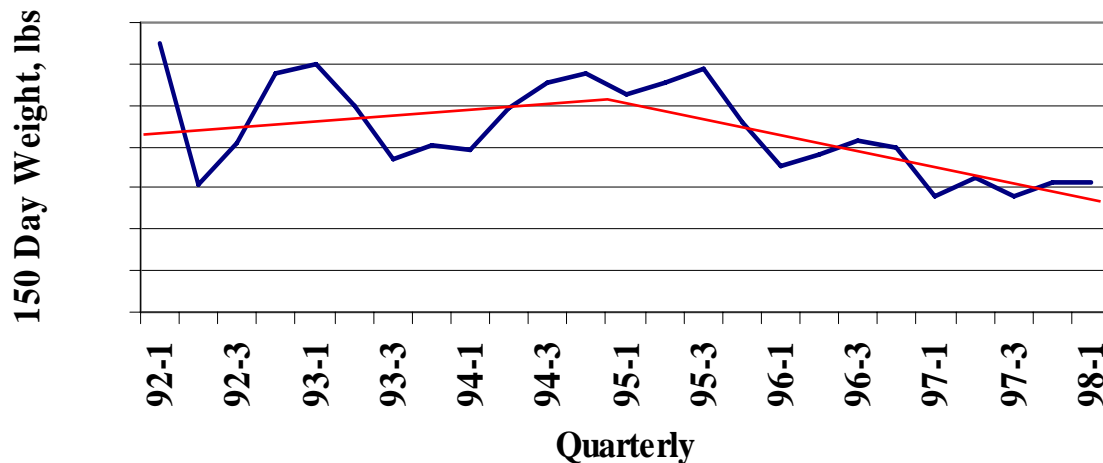


Figure 3: Response to Group Selection

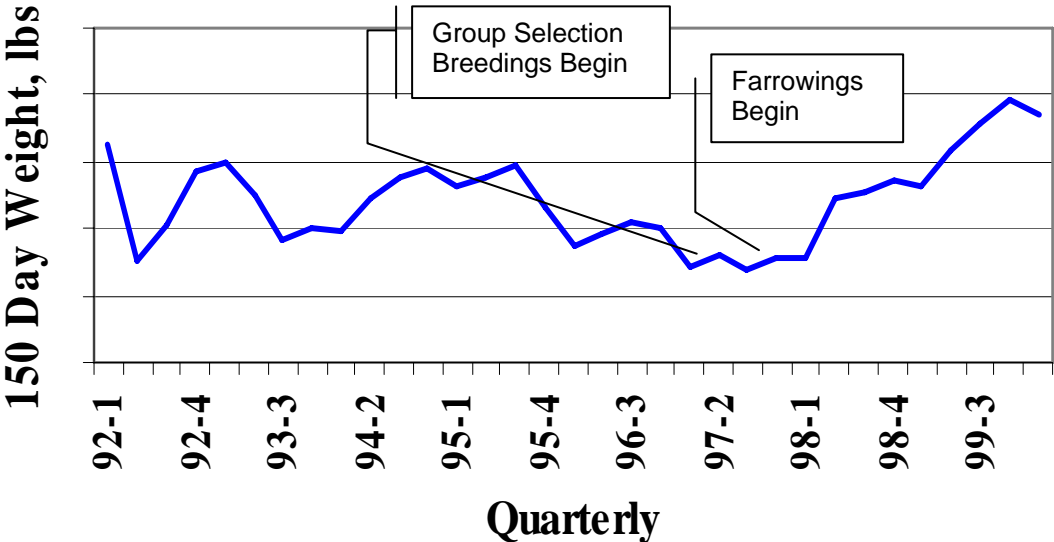


Figure 4: Interaction amongst animals in a pen.

