INCORPORATION OF COMPETITIVE EFFECTS IN BREEDING PROGRAMS TO IMPROVE PRODUCTIVITY AND ANIMAL WELL BEING

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INTRODUCTION

Over the past five decades the art of animal breeding has rapidly advanced into an exacting science with such developments as BLUP estimation of breeding values and REML estimates of variance components. These new methods promise much faster advances in genetic improvement than previously possible. However, actual responses have often fallen short of expectation and in some cases responses were worse than with previous methods. The reason for these disappointing results can only be due to assumptions inherent to the BLUP models used. The most commonly used and recognized assumption is that of an additive model, i.e. no dominance or higher order epistasis. However, a more important, and less recognized, assumption is that of non-interacting genotypes, i.e. genotypes do not compete. If higher producing animals tend to be more competitive; the effect of selection is to increase competition. Competition has the effect of lowering productivity of other animals that are in direct contention. As such, ignoring competitive interactions invalidates the BLUP model used and negates many advantages of this technology and could in fact make it a liability. Muir (1996) and Muir and Craig (1998) examined the use of group selection to address this problem and to select for adaptation of layers to multiple-hen cages. Annual percentage mortality of the selected line in multiple-bird cages decreased from 68% to 8.8% in 5 generations while eggs per hen housed increased from 91 to 237. The dramatic improvement in livability demonstrates that adaptability and well-being of these birds were improved by group selection. However group selection requires that families be housed together and selected as a group. As a result, the rate of inbreeding may increases rapidly, which would limit long term response. In this report we present a method for incorporating competitive effects in the mixed model equations, thereby allowing individual selection, and demonstrate effectiveness of this approach with a selection experiment using Japanese quail.

MATERIAL AND METHODS

Mixed Model Equations. Assume the phenotype (Y) of each animal is influenced by it's direct genetic effect (d), plus associative effects (a) from other animals in its common group, plus a random environmental effect (ε). Associative effects are genetic effects that describe how each animal impacts the performance of other animals in the group. A mixed model incorporating these effects is:

$$\mathbf{Y} = \mathbf{X}\beta + \mathbf{Z}_d \mu_d + \mathbf{Z}_a \mu_a + \varepsilon$$

where **Y** is the vector of observations, β are fixed effects corresponding to the **X**; μ_d is a vector of random direct genetic effects of each animal on its own performance, $\mathbf{Z}_d$ is an incidence matrix corresponding to each direct effect; μ_a is a vector of random associative genetic effects of each animal on performance of others in its group; $\mathbf{Z}_a$ is an incidence matrix identifying which animals are in the same group; and ε is a vector of random environmental effects. The MME are

$$\begin{bmatrix} X'X & X'Z_d & X'Z_a \\ Z_d'X' & Z_d'Z_d + k_1A^{-1} & Z_d'Z_a + k_2A^{-1} \\ Z_a'X' & Z_a'Z_d + k_2A^{-1} & Z_a'Z_a + k_3A^{-1} \end{bmatrix} \begin{bmatrix} \beta \\ \mu_d \\ \mu_a \end{bmatrix} = \begin{bmatrix} X'X \\ X'Z_d \\ X'Z_a \end{bmatrix}$$

where

$\begin{bmatrix} k_1 & k_2 \\ k_2 & k_3 \end{bmatrix} = \sigma_\varepsilon^2 \begin{bmatrix} \sigma_d^2 & \sigma_{ad} \\ \sigma_{ad} & \sigma_a^2 \end{bmatrix}^{-1}$, σ_d^2 , σ_a^2 , and , σ_{ad} are variances of additive direct, additive associative, and covariance between direct and associative effects, respectively.

Experimental Testing. Japanese quail were selected for 6 week weight based on either standard BLUP procedures (SBLUP), or Combined BLUP (CBLUP) which combines both direct and associative effects. For each line 24 sires were mated to 2 dams each and eggs collected for 14 days. Each egg was recorded and marked by mating cage to maintain pedigree information. Upon hatching chicks were brooded in full sib groups to 2 weeks of age, at which time they were wing-banded and randomly assigned to 24 growing cages, 16 birds per cage. At 43 days of age the birds were weighed and selected based on the method for each line. For CBLUP selection was based on an optimally weighted index of the direct and associate effects estimated with the CBLUP model. For SBLUP, selection was only on the direct effects estimated with the SBLUP model. After selection quail were kept in holding cages to 10 weeks of age. At 10 weeks of age breeders were culled from among those with the lowest Estimated Breeding Values (EBV's) for the method of selection and replacements made from among 10 week old birds with the highest EBV's of the same method. The process was repeated every 14 days for 28 cycles (hatches). Matings with full or half sibs were avoided. Parameters were estimated using REML from an initial two generations of random mating in the same settings without selection.

RESULTS

Selection using SBLUP failed to give any response to selection and was trending less than zero (Table 1), but not significantly so. CBLUP gave significantly better results with significant genetic gains. The lack of response to SBLUP is explained by examination of the associative (Figure 1) and direct (Figure 2) effects estimated using the CBLUP model in retrospect on both lines . While SBLUP increased the direct effects for 43 d weight, the associate effects declined. The net result was no genetic gain for weight. In contrast, selection based on CBLUP increased both direct and associative effects, although direct effects were not improved to the same extent as with SBLUP. The net effect was an increase in weight. A decrease in associative effects with SBLUP indicates that competitive effects among birds increased as selection progressed while the increase in associative effects with CBLUP indicates that competitive effects decreased.

Table 1. Linear Regression of 6 week weight on hatch number[A]

Method	Intercept (g)	Regression (g/hatch)
SBLUP	91.8 ± 4.4	-0.07 ± 0.25
CBLUP	91.5 ± 4.3	0.52 ± 0.25 *
Deviation	-0.3 ± 3.5	0.59 ± 0.20 **

[A] Regression coefficients (± s.e.); * p <0.05; **, p < 0.01

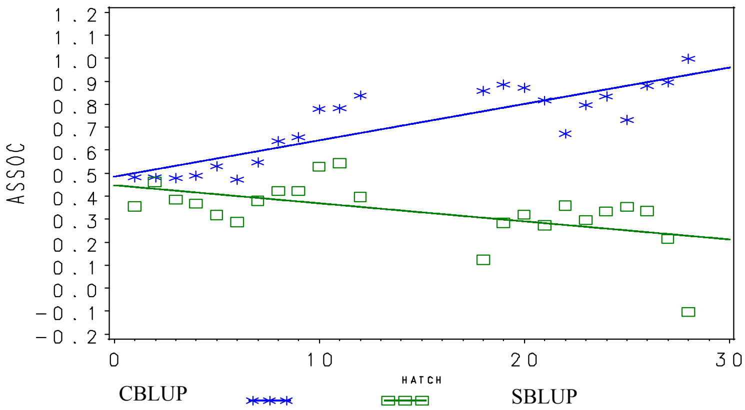


Figure 1. Associative effects estimated for each selection method by cycle of selection (hatch)

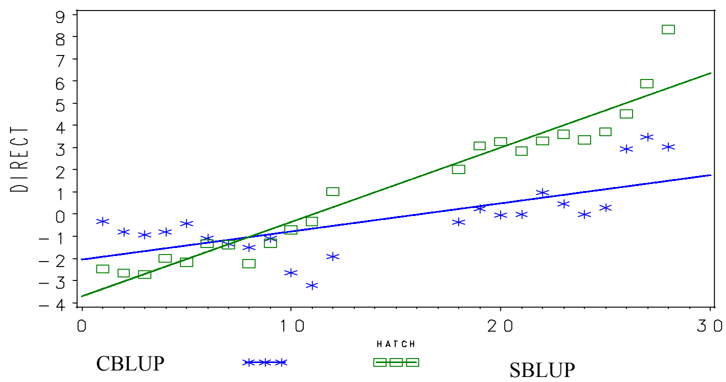
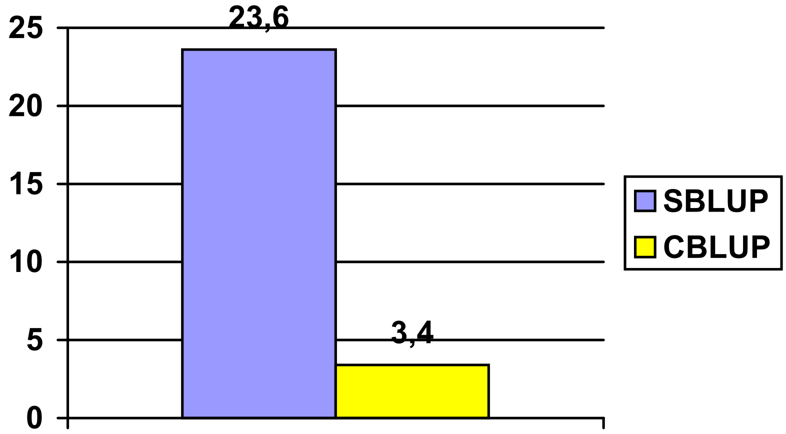


Figure 2. Direct effects estimated for each selection method by cycle of selection (hatch)

These conclusions are supported by results observed for mortalities (Figure 3).

Figure 3. Mortality (%) observed at termination of experiment



The mortality observed at the initiation of the experiment was 5%. These results show that selection using SBLUP increased aggression while CBLUP decreased aggression.

CONCLUSIONS

The incorporation of associative effects in breeding programs can result in substantially greater selection response than SBLUP if associative effects are important. These results may explain why selection in some species, such as in aquaculture, has failed to increase growth. For species in which SBLUP has been able to increase response to selection, and associative effects are known to have major effects on growth, such as with swine (Frank *et al*., 1997, Holck, 1997), these results suggest that even greater responses could be obtained if CBLUP were used. Based on past group selection in poultry and results of this trial, selection for desirable associative effects may be a means to select animals which are better adapted to their rearing environment.

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