Advances In Selection Theory Including Experimental Demonstrations: The Theory Of Selection With Social Competition

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Introduction:

Competitive social interactions among domesticated farm animals can result in injuries, stress, and mortalities, which in turn has resulted in animal wellbeing concerns for animals reared in confinement (Craig and Swanson, 1994; Swanson, 1995). A consequence of these interactions is also realized in financial losses for the producer, due to reduced growth, productivity, feed efficiency, and increased susceptibility to disease.

In pigs, the consequences of competition cause not only skin lesions, tail biting, forced withdrawals, and mortality but also the reduction in growth rate for some pen mates and consequently an increase in performance variation within pens. For example, a large variation in daily weight gain and carcass meat percentage within growing-finishing pigs was observed with one feeder for a group of 16 pigs (Botermans and Svendsen, 2000) in comparison to four feeders per pen.

In fish, several studies have shown positive phenotypic and genetic correlations between growth rate and aggression in salmonids (Huntingford *et al.* 1998; Lahti *et al.*, 2001), indicating that aggressive fish generally grow more rapidly. Another consequence of competition was lowered disease resistance (Salonius and Iwama 1993). In carp, positive selection for growth resulted in negative response presumably as a result of increased competition (Moav and Wohlfarth, 1976). Competitive interactions are not always the result of social interactions, but can be a result of passive competition for limited resources. Competition for resources among shellfish has been shown to have a strong genetic component (e.g. mussels, Brichette *et al.*, 2001; clams, Crenshaw *et al.*, 1996).

In poultry, severe social interactions can result in mortality due to cannibalism and pecking (Craig and Muir, 1998; Muir and Cheng, 2004; Muir and Craig, 1998, Ellen *et al.* 2008) as well as reduced feed efficiency (Muir, 2005).

Theory To Address Social Competition And Experimental Results

Several selection methods to address social competition have been considered, and some have proven useful, particularly in experimental settings. These methods can generally be categorized as: 1) direct selection against aggressive behaviors, 2) Multilevel selection, 3) utilization of linear models to estimate and optimally select for an animals direct and indirect genetics effects.

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Direct Selection:

This method requires direct selection on traits associated with animal well-being, such as feather pecking, tail biting, skin lesions, biomarkers, and tonic immobility (Kjaer and Hocking, 2004; Muir and Craig, 1998; Turner *et al.*, 2008). Experimental results have shown these methods to be highly effective (Craig and Muir, 1993; Kjaer *et al.*, 2001). However, application of these procedures require quantification of such traits, which can be costly and labor intensive. Further, use in breeding programs would divert selection intensity from production traits. As such, these methods have gained limited acceptance in commercial breeding programs. .

Multilevel Selection (Group Selection)

Several theoretical models have been developed to explain evolution of cooperation and altruism in natural populations. The expectation is that one could adapt a similar strategy for domestication breeding programs. Wynne-Edwards (1963; 1965) introduced group selection as a mechanism to explain social evolution. The concept was that social evolution was a result of group, rather than individual, level adaptations, where the group was defined as a set of related individuals. However, the concept of group selection as a mechanism of evolution was argued against by Maynard-Smith (1964) and Williams (1966) for two reasons. First, a stringent group structure was required, i.e. each group founded by members from one parent group and immigrants excluded from groups. Second, antagonistic within group selection was ignored which could overwhelm the between group component.

In contrast Hamilton (1964a; 1964b) introduced the concept of kin selection and inclusive fitness. With kin selection, the benefits of cooperation, and self sacrifice, are imparted to kin with which the individual interacts, at some cost to itself. Hamilton's equation basically show that altruistic (cooperative) behavior can evolve if the cost:benefit ratio is less than the relationship of the individual expressing the trait and the recipients of the benefit. i.e. the individual's genes have a better chance of being perpetuated by kin, rather than if the individual were to try to pass them on directly. Bijma and Wade (2007) showed that the two process, multilevel and kin selection, are equivalent but emphasize different aspects of social evolution, i.e. selection acting at multiple levels vs. inclusive fitness.

Nevertheless, the concerns of naturalists for kin selection and levels-of-selection modeling could easily be addressed in commercial breeding programs because group structure, mating, and selection is under the control of the breeder. Multilevel selection theory focuses on merit relative to levels of organization, exactly the same as Lush (1947) considered merit relative to between and within family deviations for non-interacting genotypes. Naturalists considered that different adaptations could occur at each level, i.e. successful individuals within a group might be highly competitive but at the group level, those with the highest merit could be those where individuals were cooperative, rather than competitive (Wade, 1977). Therein lies the appeal of selection operating at different levels of organization. The indirect genetic effects (IGE) are reflected in the group mean, thus measurement of indicator traits, such as pecking, is not necessary. Impacts of competition are directly included in the group mean to the extent the trait is impacted by social competition. Thus the potential to improve traits by considering merit at different levels of organization is apparent.

The first comprehensive quantitative genetics treatment of multilevel selection for controlled breeding programs was given by Griffing (1967; 1976; 1977) who extended the basic models for selection response to include IGEs due to social interactions or competition, which he termed associative effects. The early works of Griffing (1967) concentrated on groups of unrelated individuals however he acknowledged this could be inefficient and he later extended his methods to include related individuals with selection acting on individuals, groups, or an optimal index of within and between group deviations (Griffing, 1977). General results for predicting change in the population mean resulting from individual, group, or an index of within and between group deviations, were presented. The important features are as follows: Assume a population divided into groups of size n composed of individuals with a degree of inbreeding f and average relationships r. Let the phenotype be partitioned into that due to between and within group deviations, and let those deviations be combined in an index with weights on group deviation (τ) and within group deviations(γ), $I_{kl} = B_1 \tau_k + B_2 \gamma_{(k)l}$, then the change in the mean (u) for the index is, where truncation selection of intensity (i) is:

$$\Delta u = \left(\tfrac{i}{c}\right)\left[B_1 \operatorname{cov}(G\tau) + B_2 \operatorname{cov}(G\gamma) \right] \quad \text{where}$$

$$\operatorname{cov}(G\tau) = \left[\frac{1 + (n-1)r}{n} \right](1+f)\left[\sigma_D^2 + 2(n-1)\sigma_{DA} + (n-1)^2 \sigma_A^2 \right]$$

$$\operatorname{cov}(G\gamma) = \left[\frac{(1-r)(1+f)}{n} \right]\left[(n-1)\sigma_D^2 + (n-1)(n-2)\sigma_{DA} - (n-1)^2 \sigma_A^2 \right]$$

Thus for individual, group, and within group selection, (B_1, B_2)= (1,1), (1,0), and (0,1) respectively. The expected change in the mean for individual (I), between group (G), and within group (W) selection in non inbred (f=0) populations are given respectively by the following 3 equations

$$\Delta u_I = \left(\tfrac{i}{c_I}\right)\left[\sigma_D^2 + (n-1)(r+1)\sigma_{DA} + (n-1)^2 r \sigma_A^2 \right] \tag{1}$$

$$\Delta u_G = \left(\tfrac{i}{c_G}\right)\left[\frac{1+(n-1)r}{n} \right]\left[\sigma_D^2 + 2(n-1)\sigma_{DA} + (n-1)^2 \sigma_A^2 \right] \tag{2}$$

$$\Delta u_W = \left(\tfrac{i}{c_W}\right)\left[\frac{(1-r)(n-1)}{n} \right]\left[\sigma_D^2 + (n-2)\sigma_{DA} - (n-1)\sigma_A^2 \right] \tag{3}$$

These first two results are the same as those given by Equations 6 and 7 of (Bijma *et al.*, 2007a). Equation 1 shows that predicted response with individual selection can be negative, particularly if individuals are unrelated and the covariance between direct and associative effects is negative, i.e. a gene increase performance of the individual, but has negative impacts on the trait to others in the group. In this situation Griffing (1977) recommended that the groups consist of related individuals because as r approaches 1, within group genetic variation diminishes, while between group variation increases, and individual selection becomes equivalent to group selection, i.e. Equation 1 becomes equal to Equation 2. Equation 2, for group selection, is always positive, confirming that among group selection always improves group adaptations regardless of the sign of the genetic covariance. The disadvantage is that group selection can be inefficient, but increases in efficiency as

relatedness increases. Equation 3, for within group selection, clearly shows that within group selection can opposes between group, even if the covariance is positive. For optional response, the following index weights should be used (Griffing, 1977).

$$B_1 = \left(\frac{\mathrm{cov}(G\tau)}{\sigma_\tau^2} \right), B_2 = \left(\frac{\mathrm{cov}(G\gamma)}{\sigma_\gamma^2} \right)$$

Note that the expected change in the mean is then

$$\Delta u = \left(\tfrac{i}{c} \right) \left[B_1^2 \sigma_\tau^2 + B_2^2 \sigma_\gamma^2 \right]$$

which is always positive regardless of the parameters. Most notably, if B_2 is negative, then positive within group deviations are selected against.

Experimental Results: Wade (1976; 1977) was the first to demonstrate the power of group selection experimentally using the insect Tribolium castaneum. Goodnight (2005) and Goodnight and Stevens (1997) summarized experiments with group selection in experimental organisms. Additional experimental results were given by (Garcia and Toro, 1990; Miralles *et al.*, 1997; Wade and Griesemer, 1998). The first use of group selection in agriculture was in poultry layers reported by (Muir, 1996). Muir (1996) selected poultry layers, housed in half-sib groups, based on family hen housed egg production. Within In 6 generations mortalities were reduced from 67% to 8%, the same level of mortality as birds housed in single-bird cages. It was interesting to note that most of the response occurred within the first few generations of selection. Eggs per hen housed increased from 91 to 237 eggs, mainly as a result of increased survivability, but also the rate of lay per bird per day increased. The realized heritability in terms of response per selection difference was greater than 1 in the first generation. While a realized heritability greater than 1 is not possible in the usual quantitative genetic framework of non-interacting genotypes, Bijma *et al.* (2007a) shows that such is possible when one considers the impact of IGE on total response to selection.

In the seventh generation, the group selected and control lines were compared to a commercial line, from which the group selected line was derived. All 3 lines were housed in both single- or 12-bird cages (Muir and Liggett, 1995, Craig and Muir, 1996, Muir and Craig, 1998). Results showed that in single-bird cages, in terms of eggs per hen housed, eggs per hen per day, egg weight and egg mass, all were significantly greater for the commercial than for the group selected line, which was in turn was greater than the unselected control. However, in 12-bird cages the reverse was seen, with the selected line superior to the commercial line for eggs per hen housed, egg mass, and eggs per hen per day. The most remarkable difference was for mortality. The commercial line experienced 89% mortality at 58 wk of age as compared to the selected line with 20% and the control at 54%. The commercial line was selected based on productivity in single bird cages using essentially a Lush (1947) "optional" index, and later updated to traditional animal model BLUP (D. Harris, pers communication). In this case, the environment of selection, single bird cages, assured the assumptions of the model were correct. However, because the environment of production was the multiple bird cage, an extreme GxE resulted. Results from the commercial line also demonstrate another aspect of social evolution, even in the complete

absence of IGEs in the environment of selection, continued selection based on individual merit can be detrimental to group performance, i.e. those traits that enhanced individual productivity were inherently antagonistic to group productivity through pleiotropic IGE's that were only realized when place in a social environment.

To date, there has only been one experiment conducted to examine Griffing's (1977) suggestion that if selection based on individual merit were to be used, that interacting individuals should be placed in interacting family groups. Muir and Schinckel (2002) and Muir (2005) presented results for 25 cycles of selection for quail housed in 16 bird groups . In that experiment, two selection programs were compared, both with birds housed at random w.r.t relationship. In the 1st (AM_BLUP), traditional animal model BLUP was used based on individual merit. In the 2nd (C_BLUP), a linear model including both Direct and Associative effects was used, the theory and results for which will be presented in the next section. However there was a 3rd (Kin_BLUP) selection program (unpublished) in which traditional animal model BLUP was used, but birds were housed by half-sib family, mating 1 male to 4 females, producing an average of 4 full-sibs per female, and 16 offspring per sire family. Results showed, as previously reported (Muir, 2005) that the AM_BLUP, resulted in a negative response to selection for body weight at 6 weeks of age (BW) (-.074 ±.26g/generation), in contrast, with (Kin_BLUP), BW increased (.749±.21g/generation), the difference between programs was highly significant. Mortality increased per generation with AM_BLUP (.3±.2/generation), and decreased with Kin_BLUP (-.2±.2/generation), total percent mortality over the 25 generations was significantly (p<.0001) greater with AM_BLUP (7.7±.5%) than Kin_BLUP (5.3±.4%). Feed consumed (g) per body weight gain (g) (Feed conversion, FC) was significantly less for Kin_BLUP (.65±.02) than AM_BLUP (.76±.02). FC efficiency in Kin_BLUP was sufficient to account for energy demands of at least one additional bird per group, as compared to the AM_BLUP. These results suggest that adaptations to reduce IGEs by multilevel selection were primarily directed at improving feed conversion ratio, thereby making better utilization of limited resources and thereby increasing the number of birds that could survive.

To date there are no direct experimental results available for Griffing's (1977) optimal index, although Muir and Schinckel (2002) and Muir (2005) implemented selection on an optimal index of direct and associative effects discussed in the next section. Griffing (1977) notes that ae major disadvantage of index selection is the difficulty of obtaining reliable estimates of the genetic parameters needed to determine the weights. However, recently methods have been developed to estimate these parameters more accurately and will be discussed in the next section.

Linear Models Including Direct and IGE (Associative) Effects:

Muir and Schinckel (2002) and Muir (2005) extended the traditional mixed animal model to directly include Griffing's associative effects. With this development each animals performance can be separated into two traits, its direct and associative (IGE) breeding values. Equally important, the model allows estimation of genetic parameters via REML or MCMC such that an optimal index of those effects can be selected upon for maximal efficiency. The optimal index was shown by Muir (2005) and Bijma *et al.*, (2007b) to be a function of group size, the larger the group size the more weight that is given to the associative effects. Muir (2005) assumed independent correlation between direct and associative effects. However, Bijma *et al.* (2007b) pointed out that the assumption of

independent residuals between direct and associative effects could lead to biased estimates. . Bergsma *et al.* (2008) showed that the environmental correlation could be accounted for by including a random effect of cage in the model. Ellen *et al.* (2008) concluded that fitting either a random cage effect or a correlated residual would result the same genetic variance with positive residual covariance's among individuals in the cage. However, Cantet and Cappa (2008) examined estimability and collinearity problems with pen effects and observed that setting pen effects as random does not always remedy the collinearity problems. They suggest that the incidence matrix be written as a function of the 'intensity of competition' (IC) among animals in the same pen.

Experimental Results. Muir and Schinckel (2002) and Muir (2005) reported results conducted with Japanese quail based upon either traditional BLUP (AM_BLUP) or an optimum index of direct and IGE effects (C_BLUP). A sizable negative direct-associative genetic correlation of -0.56 was found. With C_BLUP, 6 week weight linearly increased (b=0.52 ± 0.25 g/generation) while mortality decreased (b= -.06 ± 0.15 deaths/ generation), accompanying increased efficiency of feed conversion. This was in contrast to AM_BLUP discussed above with the reverse trends.

These results verify that inclusion of associative effects in a BLUP model can address social competition in breeding programs. However it should be noted that the response from utilization of Kin_BLUP was greater than that of C_BLUP, both for weight gain and reduction in mortalities. In the Kin_BLUP line, only direct breeding values were estimated. In contrast, in the C_BLUP line, IGEs were explicitly modeled and selected for. Hence, it might seem surprising that the Kin_BLUP line showed greater response. To investigate whether this observation agrees with theoretical expectation, we approximated the theoretically expected accuracies for both schemes, using a selection index including individual and sib-information. Kin_BLUP was approximated by an index of own performance and 15 full sibs, all kept in the same group, and selection was for the ordinary EBV. Hence, Kin_BLUP ignored associative effects. C_BLUP was approximated by an index of own performance, own group members, 15 full sibs, and the group members of those full sibs, where group members were unrelated and selection was for EDBV + 15* ESBV. Hence, C_BLUP explicitly included associative effect in the breeding goal and information sources. Results showed that the theoretically predicted accuracy of Kin_BLUP (0.64) exceeded that of C_BLUP (0.36). Moreover, the correlation of the true associative BV with the EBV of Kin_BLUP (0.62) was higher than that with the associative EBV of C_BLUP (0.44). Hence, though Kin_BLUP does not specifically target associative effects, it can have higher accuracy for associative effects than C_BLUP. Kin_BLUP picks up associative effects because they are hidden in the own performance and FS-performance when group members are related. The index-weights of Kin_BLUP, **b** = [0.05, 0.29], indicate that Kin_BLUP was similar to selection based on the mean phenotype of the group, *i.e.*, group selection. The expected mean phenotype of a group, given the breeding values of the family making up the group, equals DBV + (n-1)SBV. Hence, kin-selection is close to selection for the optimum breeding goal. In conclusion, both empirical results and theory indicate that relatedness within groups is a key factor for response; the use of C_BLUP does not make relatedness superfluous. C_BLUP, however, will always outperform Kin_BLUP when applied to the same breeding structure, e.g., C_BLUP utilized with full-sib groups outperform Kin_BLUP utilized in full-sib groups. However, genetic parameters cannot be estimated with such a group structure (Bijma *et al.*, 2007b), those would have to come from another experiment were individuals were randomly allocated to groups.

Results of Muir and Schinckel (2002) have stimulated interest in this method and a number of others have perfected upon the model and utilized on a number of species. Notably, in layer chickens by Bijma *et al.* (2007b) and Ellen *et al.* (2008) on survival days; In pigs, by Arango *et al.* (2005), Chen *et al.* (2008, 2009) and Bergsma *et al.* (2008) for average daily gain (ADG) in beef cattle by Van Vleck *et al.* (2007). Brichette *et al.* (2001) directly utilized the methods outlined by Griffing (1977) to estimate direct and associative effects in shellfish.

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