Review

A general review of competition genetic effects with an emphasis on swine breeding

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ABSTRACT. A review of previous studies is presented on estimates of genetic parameters and responses to selection with traditional breeding approaches, on correlations between agonistic behavior and growth performance, and on theoretical frameworks for selection incorporating interactions among individuals and on practical methods for incorporating competition effects in breeding programs.

Key words: Behavior, Competition effects, Heritability, Review, Swine

GENETIC PARAMETERS WITH TRADITIONAL BREEDING APPROACHES

The resemblance between relatives is often measured as the covariance due to additive genetic variance. Genetic factors, however, are not the only sources contributing to the covariance between relatives. Environmental components may also increase or reduce resemblance between relatives (Falconer and Mackay, 1996). Genetic progress with classical breeding approaches has been achieved based on reliable estimates of genetic parameters (Bryner et al., 1992). Accurate genetic correlations between traits are also essential to make genetic progress. Possible sources of variation are included in statistical models to increase the accuracy of predicted breeding values. For example, the maternal genetic effect has been considered an embedded second animal effect on an individual's performance for many traits (e.g., Bijma, 2006). For production traits in swine and other livestock, estimation of direct heritability with different models and statistical methods have included maternal or litter effects. Categories of possible effects that account for variation, such as maternal and common litter effects, have been reviewed (Bryner et al., 1992; Li and Kennedy, 1994; ten Napel and Johnson, 1997; Hermesch et al., 2000; Johnson et al., 2002; Suzuki et al., 2005). Production traits examined for swine were average daily gain (ADG), average daily feed intake (ADFI), backfat depth (BF), loin eye area (LEA), and weight at 100 days (WT100).

Bryner et al. (1992) analyzed records of Yorkshire boars from central test stations in the United States with a sire-maternal grandsire model and found significant maternal effects that accounted for 23 and 11% of the variance for ADG and BF, respectively. The additive genetic correlation between BF and ADG was negative (-0.05) but close to zero. Ferraz and Johnson (1993) compared models to estimate variances of maternal and litter environmental effects for ADG and BF. Records of Landrace and Large White pigs were used. The estimate of direct heritability for ADG decreased almost 30% when litter effects were included in the model. With the model including correlated maternal and direct genetic effects and litter effects, the estimate of direct heritability for BF was 0.42 with 5% of the phenotypic variance due to common litter effects. With litter effects in the model for Large White, direct heritability estimates for ADG, ADFI, BF, and LEA were 0.24, 0.23, 0.36, and 0.24, respectively, with models including initial test age as a covariate with fixed contemporary groups and random animal and litter effects (Johnson et al., 1999). Litter effects accounted for 18, 22, 13, and 18% of the variance for ADG, ADFI, BF, and LEA, respectively.

Johnson et al. (2002) investigated postweaning growth performance for Landrace, Yorkshire, Duroc, and Hampshire pigs. Their results revealed that animal models including maternal genetic effects would provide more accurate prediction of direct genetic values than those including only direct genetic effects. For example, maternal effects were important ($P < 0.05$) for LEA and WT100 in Landrace, for BF, LEA, and WT100 in Yorkshire, for ADG and WT100 in Duroc, and for WT100 in Hampshire pigs. Litter effects were also important for ADG, ADFI, BF, LEA, and WT100 for the four breeds. They concluded that maternal effects should be included in models for genetic evaluation for direct breeding values and to improve response to selection. Chen et al. (2002) estimated genetic parameters and genetic trends from records from the National Swine Registry Swine Testing and Genetic Evaluation System. Without maternal genetic effects in models, biased estimates of direct heritability were found for growth traits for Landrace, Yorkshire, Duroc, and Hampshire pigs. The results also indicated that the accuracy of estimated breeding values increased with models that included maternal genetic and litter effects.

CORRELATION BETWEEN AGONISTIC BEHAVIOR AND GROWTH PERFORMANCE

The pork industry has improved growth performance. However, intense selection to achieve genetic growth potential may be associated with changes in behavior among grouped animals. Animal welfare concerns become an issue when some animals tend to be aggressive and cause injury under poor environmental conditions. Production efficiency could be expected to improve without compromising animal well-being by changes in the genetic selection process to include competition effects (Newman, 1994; Muir and Craig, 1998; Cassady, 2007).

Fighting mostly occurs between pigs after regrouping to establish a social hierarchy. Those agonistic characteristics may be heritable and determine social structure, such as dominance and subordination (Holden and Ensminger, 2005). The level of behavioral aggressiveness has been measured with the backtest, resident-intruder test, and lesion score for individual pigs (Hessing et al., 1993; Erhard and Mendl, 1997; Erhard et al., 1997; van Erp-van der Kooij et al., 2000; D'Eath, 2002; Ruis et al., 2002; Turner et al., 2006a,b; Cassady, 2007). Coping characteristics of individual pigs could be identified as showing either active or passive responses to stress (D'Eath and Burn, 2002). Backtest is the most often used measure of coping behavior and is related to lean gain for pigs. An individual pig is held on its back and the frequency of escape attempts (struggling bouts) is recorded for one minute. For the backtest, a genetic component is assumed (van Erp-van der Kooij et al., 2000; Cassady, 2007). The resident-intruder test is the measure of aggressiveness for a pig toward a younger unfamiliar pig. Attack latency of resident pigs is recorded when an unfamiliar intruder pig is introduced into the pen (Erhard and Mendl, 1997; D'Eath and Burn, 2002).

Botermans et al. (2000) reported more skin injuries for pigs in a highly competitive environment. Skin lesion score has been used as an indicator of post-mixing aggression in commercially housed pigs (Turner et al., 2006a). An estimate of heritability of 0.22 for lesion score was reported by Turner et al. (2006b) but with no significant genetic or phenotypic correlations between lesion score and growth rate. More studies of the genetic correlation between aggressive and growth traits are needed to evaluate the consequences for improving well-being through genetic selection (Cassady, 2007).

Studies in fish breeding have been conducted to investigate relationships between behavioral changes and selection. Competition is considered a major component of variation for individual growth rate (Rubenstein, 1981; Ruzzante and Doyle, 1991). Variation in body size for grouped fish could be a result of social structure. Agonistic behavior in fish is partially inherited and is an indirect result of selection for growth. There is little known about the response of behavior to selection for growth in different social environments. With *ad libitum* feeding, Ruzzante and Doyle (1991) reported that selection for fast growth in medaka was effective in a high density population with much social interaction. In a later study with medaka (Ruzzante and Doyle, 1993), an experiment to observe behavioral responses to selection for growth with unlimited food was conducted. Two interaction environments were provided. An environment with high interaction was designed with food positioned in the tank with limited access. A low interaction environment was designed with food spread over the surface of the container. Their results showed a negative but desirable correlation between agonistic behavior and mean growth of broods from selection for faster growth in an environment with high social interaction. They concluded that competitive individuals seem to avoid wasting energy to fight with other individuals when food is gathered in tanks but unlimited in quantity.

EXTENDED GENETIC MODELS FOR SELECTION INCORPORATING INTERACTION AMONG INDIVIDUALS

Failure to respond to selection

In the past, selection theory has been developed within the framework of non-interacting genotypes in a population. Some behavioral traits are speculated to have genetic components (e.g., agonistic behavior), which indicates that competition among individuals may have an impact on genetic evaluations. Selection based only on direct additive models without consideration of the effect of competition could overestimate the expected response to selection (Griffing, 1967; Wright, 1986). These results could partially explain why response to selection has varied or has been unpredictable in some past studies (Griffing, 1967; Kinney Jr. et al., 1970; Wilson, 1974; Garwood and Lowe, 1980; Kyriakou and Fasoulas, 1985; Clair and Adams, 1991).

For genetic evaluation using sib correlations, both genetic and environmental effects contribute to the covariance among relatives and the degree of resemblance. A brief mention of reduced resemblance between relatives in Falconer and Mackay (1996) was made to illustrate how competition effects could make the intraclass correlation among sibs meaningless. With competition effects regarded as environmental effects, resemblance of sibs can be reduced if members of the same family compete for limited feed and space. Competition effects become an additional source of variation within sib groups and result in reduced or nil variation among families. A negative intraclass correlation coefficient may reduce the benefit of best linear unbiased prediction (BLUP) (Pirchner, 1969; Falconer and Mackay, 1996).

Experiments with Japanese quail conducted by Muir and Schinckel (2002) resulted in negative responses to selection for weight based on standard models with BLUP. Mortality also increased from 5 to 24%, indicating that aggressive behavior increased with selection for weight using standard models with BLUP. In plants, a strong negative correlation between competition and yield has been documented. Kyriakou and Fasoulas (1985) applied three intensities of selection to an unselected rye population. Each resulted in negative responses for annual yield for an environment with competition among plants. Clair and Adams (1991) refer to competition due to the proximity of neighbors as density competition and the likeness of genotypes as intergenotypic competition. The results showed that distance apart and genotype of competitors had large effects on estimates of heritability and genetic gain in biomass. When both density and intergenotypic competition existed, the largest estimates of heritability were found. However, evaluation of single families planted with close spacing (only density competition was considered) resulted in the lowest estimates of heritability. One possible hypothesis (resource-partitioning) would be that a single family with like genotypes competes for the same resources. Cheplick and Kane (2004) also reported results that support the resource-partitioning hypothesis that genetically similar individuals would express the highest degree of competition compared with genetically variable individuals.

Extended genetic models incorporating interaction among individuals

A model to account for interacting genotypes within groups composed of random individuals was first proposed by Griffing (1967). The usual genetic model was extended not only for direct effects but also for interaction among other genotypes in the group. The predicted response from individual selection with regard to groups composed of random individuals of number n was

$$\Delta\mu = \left({i}/{\sigma_p} \right)\left[\sigma_d^2 + (n-1)\sigma_{dc} \right]$$

where $\Delta\mu$ is the expected change in the mean, σ_p is the phenotypic standard deviation, i is the factor for intensity of selection, σ_d^2 is the variance of direct genetic effects, and σ_{dc} is the covariance between direct and competition genetic effects. When competition effects are taken into consideration, the expected response to selection is no longer a function of non-negative quantities. As the number of competitors increases, competition effects may have more weight in the prediction of total response to selection. If direct and competition effects are negatively related, the covariance can be negative, which may result in a decrease in the progeny mean when selection is for individuals with largest estimated genotypic values. With negative genetic change in group means, continued positive selection for direct genetic effects could lead to a population mean different from its potential maximum. Wright (1977) also demonstrated the effects of competition with regression models. Response to selection was non-linear over a range of genotypes. With negative regression coefficients of associative on direct effects, response to selection would become less effective and could become negative.

More illustrations of the problem of competition on selection response were examined in a later series of papers by Griffing (1968a,b, 1969). To untangle the negative effects due to competition in response to selection, Griffing (1967) concluded that with group selection it is possible to have non-negative genetic gain under positive selection pressure, irrespective of the sign of the covariance. For randomly constructed groups of size n,

$$\Delta\mu = \left(1/n \right)\left(i/\sigma_p \right)_{gr.} \left[\sigma_d^2 + 2\left(n-1 \right)\sigma_{dc} + (n-1)^2 \sigma_c^2 \right]$$

where $\Delta\mu$ is the expected change in the mean, gr indicates that i and σ_p relate to group means and σ_c^2 is the variance of competition genetic effects. This function shows that response to selection is non-negative even with a negative correlation between direct and competition genetic effects. The greatest effectiveness with group selection would be expressed when genotypic interactions among individuals within groups exist (Griffing, 1968a).

Responses to selection based on full-sib groups and extreme forms of non-random groups were demonstrated with similar conclusions in later studies by Griffing (1976a,b). However, one exception to positive response with group selection could occur for groups of one size but with measurements from groups of another size (Griffing, 1968a).

For practical uses, prediction equations with parent-offspring covariances were formulated because these parameters were estimable (Griffing, 1968b). An index combining direct and associative phenotypic values was developed for groups containing n randomly associated individuals (Griffing, 1969). Several more recent studies have extended genetic models to include competition effects. For example, Gallais (1976) gave expressions for selection for general combining ability in plants taking into account the effect of interactions between pairs of individuals. The general combining ability, caused by additive effects and epistatic effects based on additive gene combinations, was evaluated only with the first-order interactions between pairs of genes. Expressions in terms of quadratic components describing direct and associative effects, and direct by associative interactions for individual, and between and within group variances were given by Wright (1986).

Effectiveness of group selection has been compared with individual selection (Wade, 1977; Craig, 1982; Craig and Muir, 1996; Muir, 1996). Group selection may be more efficient relative to individual selection for traits with small heritability or large environmental variances (Craig, 1982). Based on the theory of Griffing (1967), Muir (1996) addressed the question of how competition effects impact group growth in poultry. In multiple-bird cages, annual percentage mortality declined from 68 to 9% in five generations of selection for egg mass based on sire family averages. In the same time period, mortality increased from 3 to 9% for the unselected line in single-bird cages. Craig and Muir (1996) analyzed the mortality, feathering score and body weights of hens and concluded that there was no difference in feather scores among genetic stocks in single-bird cages but significantly larger feather scores for selected lines in cages with 12 birds. Livability was effectively improved by group selection. Group selection seems to have desirably improved adaptability when competition effects existed. Muir and Craig (1998) reviewed other studies and concluded that improving well-being through group selection could be effective without sacrificing productivity.

PROCEDURES INCORPORATING COMPETITION EFFECTS FOR INDIVIDUAL SELECTION WITH BLUP

Mixed model equations incorporating competition effects

Mixed model equations incorporating competitive effects for individual selection were presented by Muir and Schinckel (2002) to predict direct and competition genetic effects. The phenotype of an individual can express effects of competitors. A mixed model incorporating direct (d) and competition genetic effects (c) in matrix form is:

$$y = X\beta + Z_d d + Z_c c + e$$

where y is the vector of observations, β is the vector of fixed effects corresponding to a known incidence matrix, X, and d and c are vectors of random direct genetic effects and random competition genetic effects, respectively, Z_d and Z_c are incidence matrices for direct and competition genetic effects, and e is a vector of random environmental effects. The mixed model equations multiplied by σ_e^2 are

$$
\begin{bmatrix}
X'X & X'Z_d & X'Z_c \\
Z_d'X & Z_d'Z_d + k_1 A^{-1} & Z_d'Z_c + k_2 A^{-1} \\
Z_c'X & Z_c'Z_d + k_2 A^{-1} & Z_c'Z_c + k_3 A^{-1}
\end{bmatrix}
\begin{bmatrix}
\hat{\beta} \\
\hat{d} \\
\hat{c}
\end{bmatrix}
=
\begin{bmatrix}
X'y \\
Z_d'y \\
Z_c'y
\end{bmatrix}
$$

with

$$
\begin{bmatrix}
k_1 & k_2 \\
k_2 & k_3
\end{bmatrix}
= \sigma_e^2
\begin{bmatrix}
\sigma_d^2 & \sigma_{dc} \\
\sigma_{dc} & \sigma_c^2
\end{bmatrix}^{-1}
$$
and A^{-1}, the inverse of the numerator relationship matrix.

Note that the row of Z_c for the record of an animal will include a 1 for each competitor in contrast to only a single 1 in the row of Z_d for the record of an animal. Various extended models have been used in other studies of competition effects. For example, random pen and litter effects were included (Arango et al., 2005), random or fixed pen effects were included (Van Vleck and Cassady, 2005; Chen et al., 2006; Van Vleck et al., 2007), and environmental competition effects were included (Muir, 2005; Bijma and Muir, 2006; Muir and Bijma, 2006; Rutten et al., 2006; Bijma et al., 2007b; Chen et al., 2007; Van Vleck et al., 2007).

Estimation of genetic parameters

Simulation studies have been conducted to investigate the effect of ignoring various effects from statistical models. For example, unexpected estimates of variance components with models containing competition genetic effects were reported by Van Vleck and Cassady (2005). Standard deviations for estimates of variance of competition genetic effects were smaller with fixed pen effects rather than with random pen effects (Van Vleck, 2005; Van Vleck and Cassady, 2005). These results might have been due to the difficulty of partitioning the pen and competition variances when the pen is considered as a random effect. Large overestimation of pen variance was also observed when competition effects were ignored. The intraclass correlation assumption was used to interpret the amount of overestimation of pen variance (Van Vleck and Cassady, 2004, 2005). The variance for pens is equal to the covariance between records of any pair of animals in the same pen. With 6 unrelated animals in a pen, records of animals 1 (y_1) and 2 (y_2) adjusted for fixed effects could be presented as $y_1 = d_1 + c_2 + c_3 + c_4 + c_5 + c_6 + pn + e_1$ and $y_2 = d_2 + c_1 + c_3 + c_4 + c_5 + c_6 + pn + e_2$. Two cases are discussed below.

1) Ignore competition effects:

$Var(Pen) = Cov(y_1,y_2) = \sigma^2_{pn} + 4\sigma^2_c + 2\sigma_{dc}$ with $4\sigma^2_c + 2\sigma_{dc}$ accounting for possible bias if competition effects are ignored.

2) Ignore direct-competition covariance (fixed as zero):

$Var(Pen) = Cov(y_1,y_2) = \sigma^2_{pn} + 2\sigma_{dc}$ with $2\sigma_{dc}$ accounting for the amount of bias in pen variance.

Van Vleck and Cassady (2005) also concluded that a high estimate of pen variance from an analysis not including competition genetic effects may indicate important competition genetic effects. This agrees with the brief mention by Falconer and Mackay (1996) that competition effects would increase variation within a group and reduce resemblance between sibs within a group and also result in little variation among groups. Furthermore, estimates of other components of variance would be biased if pen or competition effects were to exist.

In pigs, estimates of heritability of competition effects appear to be very low. Cassady and Van Vleck (2004) analyzed data of Duroc-Hampshire and Landrace-Large White composite lines at 76 days of age with groups of eight pigs and a pen area of 7.4 m^2. Estimates of heritability for direct and competition effects were 0.57 and 0.01 for days to 105 kg, 0.63 and 0.02 for average daily gain, and 0.28 and 0.00 for backfat adjusted to 105 kg, respectively. For Large White growing gilts, Arango et al. (2005) reported estimates of heritability for direct and competition effects of 0.15 and 0.03 for average daily gain, respectively. Various

numbers of pigs in a pen (12 to 16) were used in their study with a pen area of 14 m^2 and on average 1.2 and 2.6 full and half sibs per pen. Slow convergence with an REML algorithm was reported. Overestimation of pen variance was observed when competition effects were excluded from the model. A random regression model to account for different numbers of pigs per pen produced similar results regardless of the choice of adjustment for pen size.

Chen et al. (2006) applied competition models for PIC selected lines with a constant number of pigs per pen of 15. The results revealed confounding of direct and competition effects when pen effects were considered to be fixed. Estimates of heritability for direct and competition effects were 0.29 and 0.01 for average daily gain with the full model with random pen effects, respectively. Similar changes in estimates of variance components when various factors were excluded from the full model were found in previous studies. The estimate of direct genetic variance, however, increased in their study in contrast to the increase in the estimate of residual variance reported by Van Vleck and Cassady (2005) when both pen and competition effects were dropped from the model. Effects of competition with different relationship structures are of interest but are difficult to study. Three designs of pen assignment for estimating competition genetic variance were simulated by Van Vleck (2005). Components of variation could be partitioned with full sibs assigned to the same pen, which challenged the assumption that full-sib litters were confounded with pens.

Van Vleck et al. (2007) examined competition effects on average daily gain of Hereford bulls with an average pen size of 30. The results also indicated confounding of direct and competition genetic effects with pens considered to be fixed effects. Overestimates of the variance component due to pen effects were also reported with competition effects not included in models. Rutten et al. (2006) introduced mixed model methodology to aquaculture breeding without observations on behavior but on body weight. They concluded that the model including competition effects functioned properly but with no evidence for competition genetic effects on body weight in Nile tilapia. For Loblolly pines, Cappa and Cantet (2006) included additive relationships among competitors and accounted for unequal number of competitors with a Bayesian approach. They reported that problems of convergence and sensitivity to starting values with REML as described by Arango et al. (2005) and Van Vleck and Cassady (2005) did not occur. This could be explained by different magnitudes of competition effects in plant versus animal data. A sizable negative genetic correlation between direct and competition genetic effects (-0.66) also suggested that ignoring competition effects could bias estimates of direct genetic variance.

Including environmental competition effects in models is another idea to consider. Van Vleck et al. (2007) reported that environmental competition effects seemed to account for nearly all of the variance attributed to pen effects for Hereford bulls in feeding pens. The same conclusion was drawn by Chen et al. (2007) using swine data. Muir (2005) pointed out that including environmental effects does not improve the estimates of the genetic effects. It may be useful to determine whether environmental variation is associated with permanent environmental competition effects or other factors. Bijma and Muir (2006) applied models with pooled direct and competition environmental effects and fitted a residual variance structure to avoid bias in estimates of the genetic variance.

Response to selection with an optimum selection index

The optimal linear selection index (I_i) combining both direct and competition genetic effects with optimal weights for individual i is

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

where $\hat{d}_i$ and $\hat{c}_i$ are predicted direct and competition genetic values with economic weights of 1 and number of competitors in a pen (n - 1), respectively (Muir, 2005; Van Vleck et al., 2007). The contribution of competition effects to the index is magnified by the number of competitors in a pen even with small competition effects. Consequently, response to selection per generation for total breeding value is (Muir, 2005; Bijma and Muir, 2006; Van Vleck et al., 2007; Bijma et al., 2007a).

Two BLUP procedures to estimate breeding values for selection of Japanese quail for 6-week weight were used by Muir and Schinckel (2002). The model for combined BLUP (CBLUP) included both direct and competition genetic effects and the model for standard BLUP (SBLUP) included only direct genetic effects. They found greater response to selection with CBLUP than with SBLUP. The linear regression coefficient (g/hatch) of 6-week weight on hatch number was significantly ($P < 0.05$) greater with CBLUP (0.52) than with SBLUP selection (-0.07). Competition among birds also increased as selection progressed with SBLUP but decreased with CBLUP. For example, the regression coefficient (deaths/hatch) of percent mortality on hatch number reported by Muir and Bijma (2006) increased with SBLUP (0.32) but decreased with CBLUP (-0.06).

The net result of applying the optimum selection index may not be to increase direct genetic effects, but to decrease the negative competition effects (Muir, 2005). Group performance is expected to be maximized with an optimal index.

Response to multilevel selection

Multilevel selection is regarded as selection operating at different levels of units, such as individuals within a pen and pens within a farm (Muir and Bijma, 2006). Selection operating on individuals within a pen could be associated with factors such as maternal effects, common environmental effects and social dominance. Selection operating on groups, referred to as group selection, would be associated with relationships across and within pens, and also common environmental effects.

Bijma and Muir (2006) and Bijma et al. (2007a) extended the theory of Griffing (1967) to quantitative genetic trait models to use for multilevel selection. Their study revealed that three important components determine response to selection with competition effects: (co)variances of direct and competition effects, degree of relatedness, and emphasis on different levels of multilevel selection. For a single trait, the observed phenotype of individual i (P_i) is composed of two unobserved effects, the direct effect ($P_{d,i}$) for itself and the summed competition effects ($P_{c,j}$) from its n - 1 penmates. A maternal effect model is similar to a competition effect model with one competitor. Both maternal and competition effects are embedded effects and involve genetic values of second animals. The model equation for competition effects broken down into additive and environmental effects is

$$P_i = d_i + e_i + \sum_{j \neq i} c_j + \sum_{j \neq i} ce_j$$

where d_i is the direct genetic effect of individual i, c_j is the competition genetic effect of competitor j, with non-genetic components, e_i and ce_j (Bijma and Muir, 2006). As both d_i and c_j may respond to selection, total response to selection (ΔT) per generation is as shown earlier to be

$$\Delta T = \Delta d + (n-1)\Delta c$$

where Δd is the response for direct breeding values and Δc is the response for competition breeding values. For each individual, total breeding value (T_i) is equal to $d_i + (n-1)c_i$ with a group size of n. Total response to selection can be rewritten as

$$\Delta T = \left[Cov(I, T) / \sigma_I^2 \right] i\sigma_I$$

where i denotes the selection intensity factor and I is an index that predicts T.

Bijma and Muir (2006) proposed an index for multilevel selection. A general expression (Muir and Bijma, 2006; Bijma et al., 2007a) for the index is

$$I_i = P_i + f \sum_{j \neq i} P_j$$

where the fraction f represents relative selection on individuals or groups. For example, $f = 0$ represents selection only on individuals, $f = 1$ represents selection only among groups, and $f < 0$ represents degree of within group selection. One case of $f < 0$ is when $f = -1 / (n - 1)$ which represents selection on the deviation of an individual phenotype from the mean phenotypic value of members within the group. Rewriting and expanding components in the formulas above result in

$$\Delta T = \left[Cov(P_i + f \sum_{j \neq i} P_j, T_i) \right] i / \sigma_I .$$

The $I_i = P_i + f \sum_{j \neq i} P_j$ can be rewritten as $(1 - f)P_i + f \sum_{j=i} P_j$.

Total response to selection can then be written as

$$\Delta T = \left[f\, Cov(\sum_{j=i} P_j, T_i) + (1 - f)Cov(P_i, T_i) \right] i / \sigma_I .$$

For $\sum_{j=i} P_j = \sum_{j=i} \left[d_j + e_j + (n-1)c_j + (n-1)ce_j \right]$,

then $Cov(\sum_{j=i} P_j, T_i) = \sigma_T^2 + (n-1)r\sigma_T^2$

and $Cov(P_i, T_i) = \sigma_{P,T} = \sigma_d^2 + (n-1)(1+r)\sigma_{dc} + r(n-1)^2 \sigma_c^2 .$

Total expected response to selection can then be expressed as

$$\Delta T = \left\{ f[(n-1)r+1]\sigma_T^2 + (1-f)\sigma_{P,T} \right\} i / \sigma_I$$

with $\sigma_T^2 = \sigma_d^2 + 2(n-1)\sigma_{dc} + (n-1)^2 \sigma_c^2$

where degree of multilevel selection is measured by f, and degree of relatedness among

associates is measured by *r*, the coefficient of relationship (Falconer and Mackay, 1996). Therefore, (co)variances of direct and competition effects (σ_d^2, σ_{dc}, and σ_c^2), the degree of relatedness (*r*), and the degree of multilevel selection (*f*) determine the response to selection when interactions among individuals exist (Bijma and Muir, 2006; Bijma et al., 2007a,b).

With individual phenotypic selection among unrelated individuals (*f* = *r* = 0), response to selection reduces to

$$\Delta T = (i/\sigma_I)(\sigma_d^2 + (n-1)\sigma_{dc})$$

which is the result given by Griffing (1967) with $\sigma_I = \sigma_P$.

With group selection alone, selection is based on the mean phenotypic value of the group,

$$\overline{P}_{gr} = (1/n)\sum_{i=1} P_i$$

(Ellen et al., 2007). Expected response to selection among groups of unrelated individuals (*f* = 1 and *r* = 0) will be

$$\Delta T = (i/\sigma_I)\sigma_T^2 = (i/\sigma_I)[\sigma_d^2 + 2(n-1)\sigma_{dc} + (n-1)^2\sigma_c^2]$$

with $\sigma_I = n\sigma_{\overline{P}_{gr}}$. This expression can be rewritten as

$$\Delta T = (1/n)(i/\sigma_{\overline{P}_{gr}})[\sigma_d^2 + 2(n-1)\sigma_{dc} + (n-1)^2\sigma_c^2]$$

which is the result given by Griffing (1967).

With competition effects, positive genetic improvement in growth by selection may not be guaranteed for some genetic evaluation systems (e.g., individual phenotypic selection and group selection with different group sizes). For individual selection, the weighted optimal index is expected to decrease negative competition effects especially when variation due to competition genetic components is not small.

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