Genetic Control of Breed and Crossbred Performance

Existing breeds or closed lines of each livestock species are essentially mildly inbred lines, whose relative straightbred performance levels are determined by differences in both 1) mean gene frequencies and 2) degrees of heterozygosity relative to a hypothetical population of all possible breed crosses for a given species. These breed differences have developed over time from both 1) deliberate and natural selection for adaptation to differing production-marketing environments and 2) random drift in gene frequencies and in degree of heterozygosity (inbreeding) from variable limits on the effective size of each breed population. These differences include average, dominant and non-allelic interaction effects of genes. Crosses of breeds or lines produce changes in performance relative to the parental stocks from complementary maternal/paternal effects, increased heterozygosity (reduced inbreeding) for dominant alleles, and from changes in non-allelic interactions as well. The challenge is to evaluate these genetic components of breeds and their crosses accurately enough to predict the performance to be expected from alternative choices of breeds and breeding systems. This task is complicated by the multiple-trait nature of the breed differences and their interactions with production environments which together determine the economic efficiency of livestock production-marketing systems.

Alternative Uses of Genetic Diversity.

Alternative uses of genetic diversity among breeds or strains of livestock include 1) expansion of the more efficient adapted breeds, 2) systematic crossing of selected breeds and 3) development of new composite breeds from selected combinations of several preexisting breeds. All three alternatives permit more rapid short-term genetic adaptation to changes in production-marketing environments than can be expected from selection within a single breed population (Smith and Banos, 1991). However, relative effectiveness of these alternative breed uses depends upon both the nature of gene effects on performance traits (average, dominant, epistatic) and the reproductive rate of the species (Dickerson, 1969, 1973; Smith, 1989).

Expansion of a superior breed simply replaces other breeds that have poorer gene-frequency and heterozygosity effects on performance. It can be accomplished by outcrossing and then backcrossing to the superior breed, and less efficiently, by reduced selection among female progeny of the superior breed (Robertson and Asker, 1951). However, ultimate improvement from this method is limited to that obtainable by continued selection within the better pure breeds, since possible further improvement from crossbreeding is ignored.

Some system of crossbreeding usually can make more effective commercial use of breed differences than "grading up" to the best adapted breed, by exploiting heterosis in individual, maternal or paternal performance, including complementary breed differences in maternal *vs* transmitted individual effects in performance (Winters et al., 1937; Lush et al., 1939; Smith, 1964; Cartwright, 1970; Moav, 1966, 1973). The alternative two- three- or four-breed specific or rotation crossbreeding systems differ not only in the proportion of the maximum heterosis used, but also in the proportion of purebred matings required to provide replacements for the industry crossbreeding system (Dickerson, 1973). 'Periodic' rotational crossing, using sire breeds in unequal numbers of generations, but in strategic sequence, has been shown to have less integenerational variation (Bennett, 1987), and to potentially equal or exceed the efficiency of conventional sire breed rotations.

Still another alternative is formation of new "composite" breeds from a combination of pre-existing breeds selected for superior adaptation to a breed-role and production-marketing system. Such composite breeds use less of the maximum F_1 heterosis than in systematic crossbreeding, and alone cannot utilize the "complementarity" of terminal crossing. However, a new composite can be maintained by the much simpler straight breeding, and does not require continued replacements from matings of parental purebreds. Desired selection may be applied more directly and intensively than in separate parental breeds. New composite breeds also can be selected to serve as specialized maternal or paternal parents in specific two-breed crossbreeding systems, thus contributing to some increased heterosis in maternal and/or paternal performance and to complementary maternal and terminal sire breed effects, with a reduced proportion of parental line matings (Cartwright, 1970; Cartwright et al., 1975). If desired, a composite breed also can be propagated and possibly further improved by continuing use of only F_1 crossbred sires from the breeds of its origin.

The ultimate choice of optimum breeding system for any given production-marketing environment depends upon the balance between the amount of heterosis and breed of sire/dam complementarity in performance efficiency achieved by the crossbreeding system and the proportion of the total industry population represented by the crossbreds (Dickerson, 1973). For this reason, systems such as rotational crossbreeding which requires only sires of pure breeds, or new multi-breed composites which require no parental purebred matings, are more efficient for species with a low reproductive rate, such as cattle. In contrast, the higher degree of heterosis and complementary paternal/maternal performance for specific two-, three- or four-breed crossing systems are likely to be more efficient for swine and especially for poultry, where a higher reproductive rate requires a relatively small proportion of purebred matings to provide replacement breeding stock for crossbreeding.

Genetic Parameters of Breeding Systems.

The relative efficiency of alternative breeding systems for use of genetic diversity among breeds is determined mainly by 1) average transmitted breed deviations in individual (g^I), maternal (g^M) and paternal (g^P) effects on progeny performance; 2) magnitude of crossbred heterosis for individual (h^I), maternal (h^M) and paternal (h^P) effects; 3) change in non-allelic gene interaction effects from non-parental recombination in crossbred progeny and parents (r^I, r^M and r^P); and 4) the reproductive rate of each species, and of breeds within a species, , which controls the proportion of purebred *vs* crossbred matings required in each industry breeding system.

The expectations for dominance effects in systems of mating were first defined by Wright (1921, 1922). He also recognized that deviations from linear association with changes in heterozygosity among parental, F_1, F_2 and backcross generations provide evidence for effects of non-allelic gene interaction (Wright, 1977). Expectations for dominance effects in rotational crossbreeding, using sires of n breeds, were given long ago by Cannon et al. (1956). Breed average transmitted direct (g^I_i), and indirect maternal (g^M_i) or paternal (e.g., in conception rate, g^P_i) effects in breed crossing can be measured in some type of diallel mating design (Table 1). Here, heterosis can be estimated for the mean of all crosses included ($h^I_.$), for those crosses having a common breed of sire (h^I_i) or dam (h^I_j), or both (h^I_i), for each pair of reciprocal crosses (h^I_{ij}) and for possible specific reciprocal sex-linked or cytoplasmic effects ($s^I_{ij}, s^I_{ij} = r^{**}_{ij}, r^{**}_{ji}$, Eisen et al., 1983). Differences between reciprocal crosses are

assumed caused by breed indirect maternal effects $(g_{\cdot j}^{M} - g_{j\cdot}^{M})$, although differences in average breed paternal $(g_{j\cdot}^{P} - g_{\cdot j}^{P})$ or in specific $(S_{ij}^{I}$ *vs* $S_{ji}^{I})$ effects also can possibly be involved. Deviations of breed average (h_{i}^{I}) or specific cross heterosis (h_{ij}) from the mean for all crosses $(h_{\cdot\cdot})$ indicate differences either in degree of change in heterozygosity (correction of inbreeding effects) or in non-allelic interaction effects, or both.

Heterosis for indirect maternal (h^{M}) or paternal (h^{P}) effects requires mating designs (Table 2) using crossbred females and/or males as parents in experimental comparisons with

purebred parents (i.e., $A \bullet (BC) - \dfrac{1}{2}(AB+AC) = \hat{h}_{BC}^{M}$, or $(BC) \bullet A - \dfrac{1}{2}(BA+CA) = h_{BC}^{P}$).

These parameters are very useful in choosing breeds for specific crossbreeding (e.g., two-, three, or four-breed) but not to evaluate the possible role of a new composite relative to rotational or specific crossbreeding systems. The latter also requires information about epistatic deviation from linear association with changes in heterozygosity that can be obtained only from designs comparing parental, F_1, F_2, F_3 and backcross generations.

The formulation used here (Table 3) expresses expectations for alternative crossbreeding systems in terms of deviations from the weighted mean of the n parental pure breeds $(\bar{p}_{n})$ where $q_{i\cdot}$ = fraction of each parental breed in progeny or parents of a given mating. The expectation for heterosis (h) includes effects of increased heterozygosity on expression of both dominance (d) and non-allelic interactions of average (gg), average × dominant (gd) and dominant (dd) gene effects in the deviation of various crosses from the mean of the parental breeds $(\bar{p})$. Thus the expected effects of non-allelic interaction on differences among various types of crosses can be expressed as deviations from the proportion of such effects included in the average F_1, heterosis of crossbreds (h = d + 1/2 gg). In this approach (Dickerson 1969, 1973; Koch et al., 1985), the r parameter measures epistatic deviations of observed heterosis from linear association with expected change in degree of heterozygosity from the mean for the parent breeds. This partition of epistatic gene effects (gg, gd, dd) agrees with that proposed by Hill (1982), except that expectations are expressed as deviations from the combined dominance and epistatic effects in the F_1 (h = d + 1/2 gg), as well as from the weighted mean of parental breeds, rather than from the F_2 generation. Also scaling was reduced by one-half. Hill's (1982) formulation, in turn, was derived from earlier work of Cockerham (1954) and Kempthorne (1957). Alternative parameters for additive, heterotic and non-allelic gene interaction effects have been developed by Harvey (1960), Eberhart and Gardner (1966), Kinghorn (1980); Sheridan (1981); Willham and Pollak (1984), and compared by Eisen (1989); and Jacobec et al. (1991).

The effects of changes in heterozygosity among alternative types of matings on expression of dominance (d) are partially confounded with those of possible non-allelic gene interaction (gg and dd). Also, the number of potential genetic parameters (Table 3) is large, especially for traits of progeny that are influenced indirectly by maternal (g^{M}, h^{M}, r^{M}) or even paternal (g^{P}, h^{P}, r^{P}) genotype (e.g., seasonal date of birth, fertility of matings). Thus experimental estimation of effects from each genetic source can be difficult. The major objective is to determine the magnitude of additive breed differences, heterosis in crossbreeding, and of deviations from expectations for purely

additive and dominant gene effects (Tables 1, 2 and 4). These effects for individual components need to be combined into the total effects on production efficiency, using the relevant economic weights (partial regressions) for component traits (Dickerson, 1982).

Efficiencies of alternative breeds and breeding systems can then be compared (Table 3), including effects of reproductive rate on proportion of purebred *vs* crossbred matings in each system. If epistatic deviations from linear association with heterozygosity are important and negative, specific crossbreeding systems will tend to be more efficient than new composites in using crossbreeding heterosis, especially if large breed differences in maternal *vs* individual performance can be exploited and if a high species reproductive rate minimizes the proportion of industry purebred matings required to produce the crossbred replacements. If deviations from dominance expectations are minor, heterosis retention in a composite can be high and choice of this alternative could approach maximum industry efficiency for species with low reproductive rate, when the composite is used as a straightbred only or as a specialized maternal stock in terminal-sire crosses (Dickerson, 1973). Systematic crossbreeding is probably impractical in much of world livestock production because it requires progeny identification by breed composition and two or more separate breeding herds or flocks. Thus use of composites often may be the most feasible approach for using breed and heterosis effects to improve production efficiency, when the costs of maintaining separate breeding herds for crossbreeding systems are considered. Continued use of crossbred sires of the parent breeds to maintain or to improve an adapted composite also can minimize parental breed costs.

Environmental Effects on Performance Ranking of Genotypes.

If the performance ranking of alternative breeds or crosses differs significantly between predictable environments (e.g., between temperate *vs* tropical climatic zones), evaluations of alternative genotypes obviously should be made within the same environment in which they are to be used (Hammond, 1947). This general principle applies in choosing genotypes for use in any predictable production-marketing system. However, selection of genotypes for use across a variety of important but random and unpredictable environments is most effective when based on average evaluations across a sample of those environments (Dickerson, 1962). In choosing genotypes for use in environments which seriously limit expression of genetic potential (e.g., for survival, reproduction, growth or lactation), economically feasible improvements in the production environment should be considered before choosing the environment in which the alternative genotypes will be evaluated. A serious mistake to be avoided is choosing breeds for use in one environment based on evaluations under another environment in which the ranking of breeds is seriously different.

Some environmental factors have obvious interactions with genetic potential. For example, differences in exposure to pathogens or parasites definitely affect the expression of differences in genetic resistance. Here, unless an alternative of immunization or eradication is possible, genetic evaluations must be done under exposure. Less extreme differences in such environmental factors as temperature, humidity, nutrient availability, reproductive management or market preferences also can change performance ranking of alternative genotypes. Alternative genotypes include both average breed transmitted effects and those from various levels of crossbreeding heterosis. In some cases, the increased average breed effect in the backcross to the higher (milk) producing breed may offset the reduction of one-half in

heterosis, compared with the F_1 crossbred (e.g., Syrstad, 1989). Finally, to be most useful, evaluations need to include effects of all important traits on the lifetime efficiency of production (e.g., mortality, culling, fertility, body size, and replacement costs rather than only first parity or survivor lactation milk records). This requires assessment of the relative economic importance of component traits, as discussed under Performance Objectives.

The appropriate experimental measure of genetic by environmental interaction is the product moment correlation (r_G) between performances for the same breed genotype (G) in the contrasting environments (Falconer, 1952; Robertson, 1959; Dickerson, 1962; Yamada, 1962; Wilson, 1974). Differences between environments in only the scaling of genetic effects do not reduce the genetic correlation. However, differences between environments in only the scaling of genetic effects do reduce the intra-class estimate of genetic correlation (r'_G) obtained from the ANOVA genetic (V_G) and interaction ($V_{GF'}$) variance components of variance because they inflate the $V_{GF'}$. component $\left(\text{ie., } r_G = \dfrac{V_G}{V_G + V_{GE}} \right)$. This underestimation of true r_G can be avoided by computing the product moment correlation separately for each possible pairing of environments, or by adjusting the interaction variance ($V_{GE'}$) for scaling effects to

$$V_{GE'} - V_{\sigma_{G_i}} = V_{GE} \text{ before calculating true } r_G = \frac{V_G}{V_G + V_{GE}}$$

(Robertson, 1959). The second alternative requires separate estimation of the total genetic σ_{G_i} within each environment. Both are more labourious than avoiding the problem by standardizing phenotypic variation within each environment before doing the ANOVA (i.e., dividing observations within each environment by the standard deviation in that environment, Dickerson, 1962).