

Design of Breed Utilization Experiments

The breeds and breeding system best suited to a given production-marketing ecosystem can be determined most efficiently by a sequence of steps:

1. Define the production-marketing system or systems most likely to be economically feasible in the foreseeable future in the geographic region involved. If more than one management system is important, interaction with several management systems may need to be included in the experimental design.
2. Use any pre-existing information concerning performance of candidate breeds and breeding systems obtained under conditions most similar to those intended, to reduce number of breeds and systems to those worthy of further evaluation.
3. Choose an experimental design suited to the additional information desired and to the availability of breed samples:
 - a. Use breed-of-sire topcross design when only sires or semen is available and/or a large number of breeds are to be evaluated. When necessary, even the less efficient, indirect comparisons of breeds or crosses evaluated at different locations can be obtained as deviations from a common sire breed or cross, using semen or embryos to produce the common control.
 - b. Use a diallel design if adequate samples of both sexes are available and a sufficiently small number of breeds is involved.
 - c. If usefulness of new composite breeds vs recurrent crossbreeding is to be evaluated, include contemporary comparison of parental purebreds with F₁, F₂, backcross and F₃ generations of crossing.
4. Sires or females sampled from the breeds compared obviously should be as broadly representative of the breed (i.e., unrelated) as possible, and in the form and at the performance level that would be available if the breed were chosen for further industry use.
5. Choose performance traits to be measured that will permit estimation of economic production efficiency for the alternative breeds and breeding systems evaluated, as discussed earlier under Performance Measures Required.
6. Pre-analyze the experiment to determine the most efficient data structure (e.g., numbers of sires, dams and progeny per dam) and total scale of experiment necessary to achieve the desired confidence limits for differences of economic importance (e.g., 5% ± 2% or less).

Factors influencing the efficiency of crossbreeding experiments have been considered by Dickerson (1942, 1969, 1973); Comstock and Winters (1942); Robertson (1959) and Solkner and James (1990, 1991). Choice of the genetic groups essential to minimize error in estimating the desired breed, heterosis and recombination parameters is more important than the optimum distribution of observations among genetic groups. Required numbers usually can be estimated from prior knowledge of heritability and variability of traits to be measured. This is illustrated in Table 5 for a 5% mean difference between any two breeds siring crosses from the same breed of dam, when the trait measured has a coefficient of variation (SD/mean) of either 20 or 10% and

heritability of $h^2 = 10\%$. These examples for cattle or sheep assume only one (1) progeny per dam, so that both the dam (D) and the within dam (W) components of variance in the SE of mean difference are reduced in proportion to the total numbers of progeny per breed of sire (n_G). The sire component ($S = 1/4 V_g$) is reduced only by number of sires sampled per breed (N_s). In this example, a difference of $5 \pm 2\%$ and $P \sim .02$ would be expected for traits with $CV = 20\%$ and $h^2 = 10\%$ when $n_G = 220$ and $N_s = 22$. If numbers of progeny per breed of sire are increased to $n_G = 280$, only $N_s = 9$ would be required for the same degree of reliability for the estimated breed difference. The desired numbers can be reached by running the trial with different sire samples over several years or locations in matings with the same breed of dam.

For traits with the lower $CV = 10\%$ but same $h^2 = 10\%$, numbers required for a $5 \pm 2\%$ breed difference would be only $n_G = 60$, $N_s = 6$. For traits with higher h^2 , required numbers would be still lower.

For pigs or poultry, the $SE (\%) = \sqrt{2 \left(\frac{W}{n_G} + \frac{D}{N_d} + \frac{5}{N_s} \right)}$, where $N_d =$

number of dams per breed. A reasonable goal for size of an experiment might be $5 \pm 2\%$ for estimated breed difference in the important trait having the highest CV and lowest h^2 .

7. Analyze results to estimate size of breed, heterosis and epistatic effects in performance traits, and of differences in net production efficiency among alternative breeds and systems of breed use.

Breed of Sire Topcross.

Some of the informative topcross mating designs are shown in Figure 1. The objective usually is to determine the potential usefulness of several exotic breeds (B, C) for crossing with one or more indigenous breeds (A). This requires estimates of individual and maternal average (g^I and g^M) and heterotic (h^I and h^M) as well as non-allelic gene recombination effects (r^I and r^M) for crosses of exotic with indigenous breeds (Table 4). Results are useful for at least preliminary choices among exotic breeds for possible 1) replacement of the native breed or breeds, 2) crossing with the native breed or breeds, or 3) development of new composite breeds. Information about heterosis in crosses among the exotic breeds would require extension of this design to include three-breed crosses or crosses of each exotic with the backcrosses to other exotic breeds (e.g., $B \times CA$ or $B \times C(CA)$), but can be done much more efficiently with diallel crossing including both males and females of the breeds involved (Table 2). Deviations of F_1 crosses from the native pure breed (A) include both average and heterosis effects - i.e., $BA - AA = 1/2 (g_B^I - g_A^I) + h_{BA}^I$ (Table 4). The difference in average transmitted effects of B from A can be estimated directly from the reciprocal backcrosses: $B(BA) - A(BA) = 1/2 (g_B^I - g_A^I)$. Thus, $BA - AA - B(BA) + A(BA) = h_{BA}^I$. The linearity of increases in additive gene effects with "percentage of blood" can be evaluated by comparing:

$$A(BA) - AA = 1/4(g_B^I - g_A^I) + 1/2h_{BA}^I + 1/2(g_B^M - g_A^M) + h_{BA}^M + 1/8r_{BA}^I$$

$$(BA)^2 - AA = 1/2(g_B^I - g_A^I) + 1/2h_{BA}^I + 1/2(g_B^M - g_A^M) + h_{BA}^M + 1/4r_{BA}^I$$

$$B(BA) - A(BA) = 3/4(g_B^I - g_A^I) + 1/2h_{BA}^I + 1/2(g_B^M - g_A^M) + h_{BA}^M + 1/8r_{BA}^I$$

Only the $(g_B^I - g_A^I)$ effect increases linearly with fraction of B in pedigree; all other expected genetic fractions are unchanged except r_{BA}^I , which is 1/4 for the F_2 (BA×BA) but only 1/8 for each backcross. Thus, BA epistatic recombination effects also can be estimated by comparing the F_2 with the mean of the two backcrosses;

$$(BA)^2 - \frac{A(BA)+B(BA)}{2} = 1/8 r_{AB}^I$$

Linearity of average gene effect difference between the exotic breeds B and C can be estimated similarly from the differences among their paired backcrosses and the F_2 inter se matings:

$$A(BA) - A(CA) = 1/4(g_B^I - g_C^I) + 1/8(r_{BA}^I - r_{CA}^I) + \text{same}$$

$$(BA)^2 - (CA)^2 = 1/2(g_B^I - g_C^I) + 1/4(r_{BA}^I - r_{CA}^I) \text{SCALESYM600} \left\{ \frac{h^I + g^M}{2} + h^M \right.$$

$$B(BA) - C(CA) = 3/4(g_B^I - g_C^I) + 1/8(r_{BA}^I - r_{CA}^I) \text{ as above}$$

Any differences between r_{BA}^I and r_{CA}^I can be estimated by comparing $(BA)^2 - (CA)^2$ with the mean for the two backcross differences = $1/8(r_{BA}^I - r_{CA}^I)$ because all other elements cancel (Table 4).

Traits of reproducing females can be evaluated in a parallel manner, using each sire of a common unrelated breed in matings with females of all the exotic × native F_1 crosses (e.g., $D \times A$, $D \times BA$ and $D \times CA$). Differences in female performance which include progeny-performance (e.g., progeny output) will contain offspring average and heterotic gene effects e.g., $1/4(g_B^I - g_C^I)$ and $1/2(h_{DB}^I - h_{DC}^I)$, that are confounded with those for the F_1 female's maternal effects (e.g., with $1/2(g_B^M - g_C^M)$ and $h_{BA}^M - h_{CA}^M$) However, separate estimates of $(g_B^I - g_C^I)$ are obtainable from the F_2 and backcross progeny contrasts described above.

Linearity of increase in maternal breed effects from increasing the fraction of exotic genes also can be estimated from crosses of the F_2 and the reciprocal backcrosses with sires of a common unrelated breed, e.g., $D \times A(BA)$, $D \times (AB)^2$ and $D \times B(BA)$. Increases in $(g_B^M - g_A^M)$ or in $(g_B^M - g_C^M)$ with change from 1/4 to 3/4 B or C genes will correspond to those for $(g_B^I - g_A^I)$ or $(g_B^I - g_C^I)$ and $(r_B^I - r_A^I)$ or $(r_B^I - r_C^I)$ shown above for the F_2 and backcross progeny. The parallel effects on $(g_B^I - g_A^I)$ and $(g_B^I - g_C^I)$ of progeny from the matings with F_2 and backcross females will be exactly one-half of those for $(g_B^M - g_A^M)$ and $(g_B^M - g_C^M)$; but will also include proportional 1/4 to 3/4 increases in h_{DB}^I and h_{DC}^I proportion of total h^I heterosis. Again, importance of non-allelic gene interaction effects (e.g., r_{BA}^M or r_{BA}^I) can be estimated by comparing means of D crosses with the F_2 vs those with the two backcrosses of each exotic breed.

Diallel Crossing.

Compared with topcrossing exotic breeds on a common indigenous breed population, a diallel mating design permits estimation of heterosis among all $n(n-1)/2$ pairs of breeds instead of only n exotics with the base breed. However it requires representative samples of both males and females of each breed. Thus, it is useful

mainly for evaluation of breeds already indigenous to a region or for a limited number of breeds chosen on the basis of prior topcross evaluation.

As shown in Table 1, diallel matings involve reciprocal crosses between each pair of breeds plus the contemporary pure breed matings. This first phase permits estimation of breed individual (g^I) and maternal (g^M) effects as well as heterosis for individual progeny performance (h^I), as deviations from the unweighted mean (P_n) of the n pure breeds evaluated. Each pure breed mean includes the general purebred mean (P_n) plus that breed's

genetic deviations for individual (g_i^I) and maternal (g_i^M) effects, where

$$\sum_i^n g_i^I = \sum_i^n g_i^M = 0.$$

Individual (h^I) heterosis can be estimated for each reciprocal cross ($h_{ij} = 1/2(X_{ij} + X_{ji} - P_i - P_j)$) and for all $2(n-1)$ crosses involving sires or dams of a given breed:

$$\bar{h}_i = \sum_j^{2(n-1)} X_{ij} - (n-1)P_i - \sum_j^{n-1} P_j \text{ or } \sum_j^{n-1} h_{ij} \text{ SCALESYM125}/(n-1).$$

Mean heterosis for all crosses, of course, is simply

$$\bar{h}_{..} = \sum_i^{n(n-1)} h_{ij} \text{ or } \bar{X}_{n(n-1)} - \bar{P}_n.$$

Effects of any new non-allelic gene interactions in the first crosses are included in the estimates of F_1 heterosis (h^I).

Average maternal effect of each breed (g_j^M) is estimated as the average difference between the dam and the sire effect of reciprocal crosses:

$$\hat{g}_j^M = \sum_i^{n-1} (X_{ij} - X_{ji}) \text{ SCALESYM125}/n, \text{ because } \sum_i^n g_i^M = 0, \text{ and } g_j^M = - \sum_i^{n-1} g_i^M,$$

so that

$$(n-1)g_j^M - \sum_i^{n-1} g_i^M = ng_j^M.$$

To obtain estimates of heterosis for maternal effects on progeny performance (h^M) requires Phase 2 comparisons of females of each reciprocal cross and of the two pure breeds both mated to the same breed of sire (Table 2), and preferably to the same sires (e.g., $1/2(D(AB)+D(BA)-DA-DB) = \bar{h}_{AB}^M$). Such contrasts for each set of female reciprocal crosses provide an estimate of $h_{ij}^M + 1/8 r_{ij}^I$, where r_{ij}^I represents possible additional non-allelic gene recombination effects in progeny that are not included in definition of h_{ij}^I . If the r_{ij}^I effects should be real and negative, they would cause an underestimate of h_{ij}^M , and vice versa.

The reality of r_{ij}^I effects can be estimated by extending the matings to include comparisons of the F_2 generation of each F_1 cross with the mean of the two reciprocal backcrosses, as shown in Table 4 for the topcross designs.

Evaluation of r^M requires comparison of F_2 females with mean of reciprocal backcross females all mated to the same sire breed, e.g., $D(BA)^2 - [D(A \bullet BA) + D(B \bullet BA)]/2$, as shown in Table 4. The value of such phase 3 matings will depend upon accumulated evidence concerning the importance of such epistatic

deviations from only average plus dominant gene effects for each species of animals and the traits of interest.

Usefulness of a new composite breed can be determined most directly by comparing the F_3 progeny (from F_2 sires and dams) with the weighted means of the purebreds and of the F_1 crosses represented in the composite (Table 3). However, wise choices between systematic crossbreeding vs new composite breed formation, as well as breed composition of the composite, require the prior information about individual and maternal breed (g^I and g^M), crossbred heterosis (h^I and h^M) and epistatic recombination (r^I and r^M) effects on production efficiency. Use of such information, plus the reproductive rate of the species, in production system evaluation should clarify possible justification for forming new general purpose or specialized maternal and paternal composite breeds. Optimum proportional representation of breeds in a composite can be predicted from the estimates of breed and heterosis effects on component traits as illustrated by MacNeil (1987).

Other Breed Comparisons.

A variety of less complete comparisons of breeds or crosses are also useful. These include growth, carcass and feed utilization tests of market meat animals; growth and feed utilization of breeding males; egg production, quality and feed efficiency of laying hens; meat, wool or fiber production, quality and feed efficiency of sheep or goats, etc. In such tests, the entries are samples of specific breeds or strain crosses. The information is helpful to potential users of the breeding or commercial stocks compared. It is also used by breeders to compare their stocks with those of other breeders. In either case, usefulness of the comparisons depends on representative sampling of each stock and the completeness and accuracy of performance information obtained. Entry of selected-samples by breeders can bias results obtained. Differences in health background of entries also can be a problem. Information from such comparative tests can be useful in selecting breeds or crosses for more complete evaluation experiments.

In several livestock species (i.e., dairy and beef cattle, sheep and swine), the genetic analyses of field (on farm) records also can provide excellent preliminary information on breed characteristics.