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Evaluation of breeds and crosses of domestic animals

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MANUAL FOR EVALUATION OF BREEDS AND CROSSES OF DOMESTIC ANIMALS

INTRODUCTION

The purpose of this manual is to suggest practical guidelines for evaluating the usefulness of available breeds or strains of livestock species and their crosses under diverse world production-marketing environments. For many years much attention has been focussed on performance comparisons among breeds and their crosses (see indexes of Animal Breeding Abstracts). This emphasis is justified because genetic differences among breeds or strains are large relative to genetic variation within breeds, (e.g., Cundiff et al., 1986). These differences are an important potential source of genetic improvement in the efficiency of human food production from livestock through 1) expansion of superior breeds, 2) gains in performance from complementary breed effects and heterosis in crossbreeding, 3) development of superior new breeds from selected combinations of several breeds, and 4) preservation of potentially useful genetic stocks that are in danger of extinction.

The enormous number and variety of local breeds and strains of each livestock species (Phillips et al., 1945; Cheng, 1984; OAU, 1985; FAO, 1986; Mason, 1988; Maule, 1989; Crawford, 1990) has developed over very long periods of time. This diversity has developed partly from both natural and artificial selection for performance (Mason, 1973) under diverse world production-marketing environments (Phillips, 1961), and partly from cumulative random changes in gene frequency in relatively small local populations (Lush, 1946; Wright, 1948).

Patterns of human and accompanying migrations have limited the sampling of potentially useful breeds available in any given geographical region, (Stonaker, 1961), and still do, in spite of recent improvements in world-wide communication and transportation. Animal health and trade restrictions also continue to be serious constraints on movement of livestock between countries (CAST, 1984). However, improvements in diagnostic tests for safe movement of animals or frozen semen and embryos are gradually easing these limitations (O.I.E. 1985).

The other serious limitation on effective current and future use of world animal genetic resources is the lack of adequate information on relative performance abilities of alternative genetic stocks under the variety of existing and potential major world production-marketing environments (ecosystems). Feasible improvements in poor production environments also need to be evaluated to allow optimum use of genetic potential (Hammond, 1947, 1949; Dickerson, 1970; Donald, 1973). The problem is how to identify those breeds, wherever located, that are best suited to future needs of each region, and to learn how they may be used most efficiently in producing animal products (Lee and Phillips, 1948; Phillips, 1967; Dickerson, 1969, 1973; Duarte, 1989; Smith, 1989).

Most efficient use of world-wide animal genetic resources in any given country or region would seem to require:

1. Careful definition of performance objectives for the species, considering the economic effects of both production costs and market prices expected under likely future production-marketing systems.

2. Identification and adequate sampling of the more promising indigenous and exotic breeds, based upon existing information.
3. Designing and conducting experiments to determine which breeds and methods of using them are likely to permit greatest gain in efficiency under the economically feasible production/marketing environments.
4. Implementing live or cryopreservation of any endangered genetic stocks shown to be of likely future value.

Bio-economic Performance Objectives in Livestock Production

The comprehensive objective in livestock improvement surely is more efficient conversion of plant feeds into animal products useful to mankind (Byerly, 1967). The problems are to predict the future relative values of animal products and costs of inputs, and what changes in biological characteristics of animals will contribute most to reduction in costs per equivalent value unit of animal product (Lerner and Donald, 1966; Dickerson, 1970; Harris, 1970). Costs, rather than profits, are emphasized here because prices tend toward total costs per unit of production, making realized profit an illusory criterion (Melton et al., 1979). Only when product prices are assumed to remain constant do "profit" and cost per value unit of output provide equivalent rankings for economic efficiency of animal production (Moav, 1973; Brascamp et al., 1985.; Smith et al., 1986). Even then, proportional changes in the real efficiency of production are greatly exaggerated by changes in the "profit" projected for reduced costs at a fixed price per value unit of output (Dickerson, 1970, 1976, 1982).

Efficiency, in terms of cost per value-equivalent unit of output from a livestock production system, is influenced not only by the genetic potential for performance of the animals in the chosen breeding system, but also by environmental effects of climate, exposure to diseases or parasites and feed resources, by the management system and by relative prices for inputs and outputs. Thus, the expected effect of genetic changes in potential performance on efficiency of production must be estimated for the particular total production-marketing environment in which the genetic potential of the animals is expressed (Hammond, 1947). This requires computer simulation of the production-marketing system, using the best information available from past research to predict effects of alternative genetic changes and breeding systems on input costs and output value (e.g., Tess et al., 1983a). The economic weighting of component traits, especially in meat production species, will differ for terminal sire *vs* maternal breed roles in crossbreeding (e.g., Bennett et al., 1983). Thus, choice of specialized breed role in crossbreeding influences the relative economic weights for most effective within-breed selection. Also, whenever the alternatives compared differ in the time frame of inputs and/or outputs, comparisons should be based on discounted costs and returns, using net rate of interest (actual less inflation rate, Dickerson, 1976; Smith, 1978; Melton et al., 1992).

The relative economic importance of component performance traits in choosing among alternative breeds or breeding systems can be estimated from the partial regressions of efficiency (E) on genetic change *(*Gi*)* in each of the component traits (b_{EG_i}), where E is cost/output unit from the specified production-marketing system (Dickerson,' 1982). These partial regressions can be estimated using computer simulation models, by evaluating effects on E from changing G for each component trait separately. Values for _ b_{EG_i} for any component trait will decline with increasing mean genetic level for the trait (G), especially when the reduction in cost/unit of output arises from spreading fixed costs over more units of output, as for breeding female costs over more progeny or for body maintenance costs over faster growth rate. For examples of calculating economic weights of component traits, see Tess et al. (1983b) for swine and Wang and Dickerson (1991) for sheep.

If the effect of one trait is modelled to include its environmental effect on a second trait, as for effect of litter size born on viability or weaning weight in pigs, care must be taken to model effects of genetic change in the second trait with the primary trait (litter size) held constant. Then in using these partial regressions in multiple-trait index selection among breeds or breeding system, values for the second trait must be first adjusted to a constant primary trait basis, and the environmental association excluded from any estimated genetic association between the two traits used in the index construction. If accuracy of breed and breeding system evaluation is high (i.e., $h\frac{2}{x}\text{SCALESYM500} \to 1$ for breed or system means) only the partial regressions (b_{EGi}) on change in each trait breeding values ΔG_i are required to predict genetic change in efficiency, $(\Delta G_e)\left(\text{i.e., SCALESYM100}\Delta\widehat{G}_e = \sum_{i}^{n}(\text{SCALESYM100}\Delta\overline{G}_i \bullet b_{EG_I})\right)$. If heritabilities of breed or system means for traits are appreciably less than perfect $(h\frac{2}{x} < 1)$, then use of both the estimated heritabilities of trait means and the genetic and phenotypic correlations among traits also are required to construct the most accurate multiple-trait index for predicting the genetic differences in efficiency (Hazel, 1943).

Performance Measures Required

General.

The cost of animal products depends primarily upon the efficiency of three basic biological functions: 1) reproduction and viability, 2) female product output and 3) rate and composition of growth (Dickerson, 1970, 1976, 1990; Harris, 1970). Total costs can be separated into two major categories: 1) for the producing and reproducing female population and 2) for growing weaned or hatched progeny to market age or weight. Product output similarly comes either 1) directly from the females - as milk, wool or eggs, or 2) from market value of progeny - as meat. Overall efficiency is measured by the ratio of total costs to product output, in economic equivalents, over a given period of time for the production-marketing system (E).

Average costs per female-year include those for replacements, R = (cost of a replacement female less average return per culled or dead female)/(mean number of years of herd or flock life), plus those of a breeding female (d) for fixed labour, housing and other (I_d), variable maintenance feed (F_{md}) and variable feed above maintenance for production (F_{pd}). Costs per female year for each of N progeny (o) from weaning to market include average daily costs for fixed items (I_o), variable maintenance feed (F_{mo}) and variable above-maintenance feed for growth (F_{po}), all multiplied by days of postweaning growth (D), plus fixed costs for marketing, slaughter, vaccines, etc. (S_o). Yearly output per breeding female includes units of direct output (e.g., milk, wool or eggs) multiplied by value/unit ($P_d \bullet V_d$) plus the product from N market progeny of P_o weight and V_o value/unit weight. Thus overall efficiency in terms of cost/unit of output value can be visualized as:

$$E = \frac{\text{Cost}/\text{yr}}{\text{Output}/\text{yr}} = \frac{(R + I_d + F_{md} + F_{pd}) + N \bullet D(I_o + F_{mo} + F_{po}) + N \bullet S_o}{P_d \bullet V_d \qquad + \qquad N \bullet P_o \bullet V_o} \quad (1)$$

It is sometimes convenient to express output values in terms of equivalent value units (e.g., as feeder calf weight from both calves and cull cows marketed, or as market lamb weight from lambs, cull ewes and wool sold). Input costs are best expressed in monetary units based on quantities and cost per unit (e.g., F_{md} = units of feed for maintenance × cost/unit, plus F_{pd} units of feed for milk or egg production × cost/unit, and similarly for maintenance = F_{mo} and gain = F_{po} of market progeny). If replacement females are produced within the herd, R = (postweaning to breeding cost-income from a culled female divided by mean cow herd life).

Input/output efficiency (E, Formula 1) can be calculated for herds or flocks at equilibrium age composition over a typical period of time (e.g., year). Thus differences in timing of costs and income are minimal, and consideration of differences in discounted costs *vs* income are not important for comparisons among breeds for a given role in a production system. However, there can be real differences among breeding systems in the timing of input costs *vs* output income (e.g., straightbred *vs* terminal sire × maternal F_1 crossbred female) that may justify including the discounting of expense and income to the same point in time for the systems compared.

The performance information required for evaluating breed and cross differences in efficiency include both outputs and inputs. Outputs are much more easily and frequently measured. However, differences in output alone greatly exaggerate the real differences in efficiency, because increased output also increases inputs, especially of feed intake.

Measures of Output.

Among traits affecting output, the very important ones for meat animals are those controlling N, the number of progeny marketed per female maintained. Increasing N directly reduces costs per unit of meat output for replacements (R) and for breeding female maintenance (F_{md}), costs that are proportionately so much greater for species with low (e.g., cattle) than with high (e.g., poultry) reproductive rate. Traits controlling N include fertility, parturition interval, number of young per parturition and viability of young. Viability may also be affected by the female's maternal ability in terms of ease of parturition, temperament and especially milk production. Other measures related to reproduction that can be important in difficult environments include those for tolerance of heat or cold, resistance to ticks and diseases, and ability to maintain body condition under sparse or variable nutrient environments. The other meat output components, of course, are the weight (P_o) and the value per unit of weight (V_o) for each market animal, the latter indicated by measures of conformation and especially composition and eating qualities.

Output from culled adult females also reduces the net cost for young female replacements (R), which is determined by adult mortality and culling for infertility or other failures, and the relative unit value of young *vs* adult cull female weight. These factors also determine the optimum terminal age and severity of culling for infertility of breeding females (e.g., Núñez-Dominguez et al., 1992), which differs greatly among species.

Measures of output from the female herself also include both quantity (P_d) and unit value (V_d) of such products as milk, fiber and eggs. A wide variety of measurements is usually required to estimate value per unit of adult product output (V_d) (e.g., composition of milk, wool character, egg size and quality).Generally, in species maintained for such specialized direct female output (e.g., dairy cattle, water buffalo, sheep, goats, egg chickens), the total value of such direct output may make income from progeny quite secondary. However, the relative importance of direct and progeny output varies greatly with the production-marketing system, from specialized meat or milk to dual purpose.

Measures of Input

Feed intake is the major measure of input cost required in comparing breeds and their crosses, but is much more difficult to obtain than measures of output, especially for breeding females of ruminant species. Feed intake for female maintenance ($F_{md)}$ varies most with her body size and that for market progeny output $(N \bullet P_o)$ varies with progeny number (N), body size maintained (F_{mo}) and rate of growth (F_{po}) over days in the feeding period (D).

To the extent possible, direct measurement of feed intake is preferable to indirect estimates of feed intake, because it involves fewer assumptions. However, especially for grazing females of ruminant species, it is often necessary to estimate feed intake from experiments with subsamples of each breed or cross, or indirectly from measures of body size and composition plus product volume and composition, using prediction formulas based upon extensive published results of prior research on energy metabolism (e.g., Graham, 1967; Koong et al., 1985).

Direct measurement of feed intake for progeny from weaning (or hatching) to market, is generally preferable and often feasible, except when growing performance is measured on pasture. When feed intake cannot be measured directly on growing market animals, it can be estimated from body weights over the feeding period.

Accuracy of feed intake estimates can be improved by obtaining body composition and/or calorimetry measures of fasting heat production for subsamples from each breeding group evaluated (e.g., Baker et al., 1991). Such basic experiments with subsamples, including indirect or direct calorimetry, permit detection of possible differences in maintenance requirements and its association with body size and composition (Olthoff and Dickerson, 1989). Non-feed costs for such items as labour, housing, health care, interest on capital tend to be only partially proportional to feed inputs. Estimates of changes in these costs with increases in components of performance should be included in evaluations to avoid upwardly biased evaluation of genetic effects on production efficiency. Improvements in such traits as fertility and mortality reduce feed and other costs more than gains in female egg or milk production or growth rate of market meat animals.

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 $(g^M_{.j} - g^M_{j.})$, although differences in average breed paternal $(g^P_{j.} - g^P_{.j})$ or in specific $(S^I_{ij}\ \textit{vs}\ S^I_{ji})$ 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 $(h_{..})$ 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., $A \bullet (BC) - \frac{1}{2}(AB{+}AC){=}\hat{h}^M_{BC}$, or $(BC) \bullet A - \frac{1}{2}(BA{+}CA){=}h^P_{BC}$).

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 $q_{i;}$ = 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 $\left(\text{ie., } r_G = \frac{V_G}{V_G + V_{GE}} \right)$. 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 $V_{GE'} - V_{\sigma_{G_i}} = V_{GE}$ 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).

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 F_1, F_2, backcross and F_3 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 ± 2% and P ~ .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 ± 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 $\mathrm{SE}\ (\%) = \sqrt{2\left(\frac{W}{n_G} + \frac{D}{N_d} + \frac{5}{N_s}\right)}$, where N_d = number of dams per breed. A reasonable goal for size of an experiment might be 5 ± 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×CA or B× 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., $BA - AA = 1/2\ (g^I_B - g^I_A) + h^i_{BA}$ (Table 4). The difference in average transmitted effects of B from A can be estimated directly from the reciprocal backcrosses: $B(BA) - A(BA) = 1/2\ (g^I_B - g^I_A)$. Thus, $BA - AA - B(BA) + A(BA) = h^I_{BA}$. The linearity of increases in additive gene effects with "percentage of blood" can be evaluated by comparing:

$$A(BA) - AA = 1/4(g^I_B - g^I_A) + 1/2h^I_{BA} + 1/2(g^M_B - g^M_A) + h^M_{BA} + 1/8r^I_{BA}$$

$$(BA)^2 - AA = 1/2(g^I_B - g^I_A) + 1/2h^I_{BA} + 1/2(g^M_B - g^M_A) + h^M_{BA} + 1/4r^I_{BA}$$

$$B(BA) - A(BA) = 3/4(g^I_B - g^I_A) + 1/2h^I_{BA} + 1/2(g^M_B - g^M_A) + h^M_{BA} + 1/8r^I_{BA}$$

Only the $(g^I_B - g^I_A)$ effect increases linearly with fraction of B in pedigree; all other expected genetic fractions are unchanged except r^I_{BA}, 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;

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

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:

$$A(BA) - A(CA)=1/4(g^I_B - g^I_C) + 1/8(r^I_{BA} - r^I_{CA}) + \text{same}$$

$$(BA)^2 - (CA)^2 = 1/2(g^I_B - g^I_C) + 1/4(r^I_{BA} - r^I_{CA})\text{SCALESYM600\}}\frac{h^I + g^M}{2} + h^M$$

$$B(BA) - C(CA)=3/4(g^I_B - g^I_C) + 1/8(r^I_{BA} - r^I_{CA})\text{ as above}$$

Any differences between r^I_{BA} and r^I_{CA} can be estimated by comparing $(BA)^2$-$(CA)^2$ with the mean for the two backcross differences = $1/8(r^I_{BA} - r^I_{CA})$ 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 x native F_1, crosses (e.g., D×A, D×BA and D×CA). Differences in female performance which include progeny-performance (e.g., progeny output) will contain offspring average and heterotic gene effects e.g., $1/4(g^I_B - g^I_C)$ and $1/2(h^I_{DB} - h^I_{DC})$, that are confounded with those for the F_1 female's maternal effects (e.g., with $1/2(g^M_B - g^M_C)$ and $h^M_{BA} - h^M_{CA})$ However, separate estimates of $(g^I_B - g^I_C)$ 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×A(BA), D× $(AB)^2$ and D×B(BA). Increases in $(g^M_B - g^M_A)$ or in $(g^M_B - g^M_C)$ with change from 1/4 to 3/4 B or C genes will correspond to those for $(g^I_B - g^I_A)$ or $(g^I_B - g^I_C)$ and $(r^I_B - r^I_A)$ or $(r^I_B - g^I_C)$ shown above for the F_2 and backcross progeny. The parallel effects on $(g^I_B - g^I_A)$ and $(g^I_B - g^I_C)$ of progeny from the matings with F_2 and backcross females will be exactly one-half of those for $(g^M_B - g^M_A)$ and $(g^M_B - g^M_C)$; but will also include proportional 1/4 to 3/4 increases in h^I_{DB} and h^I_{DC} proportion of total h^I heterosis. Again, importance of non-allelic gene interaction effects (e.g., r^M_{BA} or r^I_{BA}) 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-l)/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 $\sum_i^n g_i^I = \sum_i^n g_j^M = 0.$

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-l) crosses involving sires or dams of a given breed:

$$\bar{h}_i = \sum_1^{2(n-l)} X_{ij} - (n-1)P_i - \sum_1^{n-1} P_j \text{ or } \sum_1^{n-1} h_{ij}\text{SCALESYM125}/(n-1)\,.$$

Mean heterosis for all crosses, of course, is simply

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

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:

$$\hat{g}_j^M = \sum_1^{n-l}(X_{ij} - X_{ij})\text{SCALESYM125}/n, \quad \text{because } \sum_1^n g_j^M = 0, \text{ and } g_j^M = -\sum_1^{n-1} g_i^M,$$

so that

$$(n\text{-}1)g_j^M - \sum_1^{n-l} g_i^M = ng_j^M\,.$$

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., $1/2(D(AB)+D(BA) - DA - DB) = \bar{h}^M_{AB}$. 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●BA)+D(B●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.

Statistical Analyses of Experimental Data

General.

Analysis of well designed breed evaluation experiments is relatively simple compared with genetic analyses of field data, where more complex adjustments for environmental variables are required. Good design minimizes possible sources of error affecting the critical contrasts of genetic groups, such as age of animal, year, season or other environmental effects. Error for breed comparisons includes genetic variation among sires and dams sampled from each breed. Because results are intended to guide future choices among breeds, it is essential that the sires and dams sampled from each breed be representative and large enough in number to minimize error in detecting breed and heterosis effects. If the sires sampled from each breed for a crossbreeding experiment have also been used extensively in an industry progeny testing system, it may be possible to use their expected progeny differences to adjust the experimental ranking of breeds to the mean for each breed and for any genetic trends to a common time period (Notter and Cundiff, 1991).

Certain genetic (e.g., heterosis) comparisons even can be made between matings by the same sires and from dams by the same sires (e.g., A(BC)–AB + A(CB)–AC, Table 2, when the same sires are also used to produce the BC and B or CB and C ♀, Table 1). In this extreme case, error degrees of freedom would be those for interaction between sires of progeny and sires of dams, plus residual.

A range in fractions of individual and maternal breed and heterozygosity effects are represented among the means for the pure breeds and crosses in a well designed breed evaluation experiment. The volume of data also may vary among the breeding class means. Thus use of a linear regression model to estimate effects of each genetic parameter may be more efficient than fitting constants for each breed group (Batra and Touchberry, 1974; Robison et al, 1981).

Adjustment for Non-genetic Variation.

Variation in non-genetic influences increases the sampling error of genetic comparisons. Variation among years or seasons can be avoided by basing genetic comparisons on variation within years or seasons. Variation within years or seasons from such influences as age at measurement or parity may be reduced by linear or quadratic covariate adjustment appropriate to each genetic class, if interaction with genetic class is important. In some cases adjustment may be made most accurately by using the information for each individual, as for weight at a standard weaning age. Because early growth is nearly linear with age, weaning weight of lambs or pigs is accurately predicted from weight at birth and a variable age at weaning as, e.g., birth weight + 56x (daily gain to weaning). Covariate adjustment assumes that the environmental factor has the same influence on each individual within a genetic interaction subclass. Thus, the covariate adjustment, for example, may satisfactorily remove age bias in comparison of genetic groups, but may under-adjust the larger or faster growing individuals and over-adjust the smaller or slower growing animals.

Care should be taken to avoid adjusting for variable influences which are really part of the genetic performance being measured. For example, adjustment of mortality in piglets, lambs or even cattle for litter size or individual weight at birth helps to partition breed differences in survivability, but would be obviously misleading if applied to breed differences in numbers or weight per litter weaned. Similarly, adjusting postweaning gain or feed/gain for midweight removes not only the effect of initial weight (W_i), but also the effect of differences in daily gain, because midweight $\approx W_i + 1/2$(daily gain x length of a nearly constant growth period). Other examples are adjustment of milk records to a common length of dry or lactating period, and adjustment of carcass composition to a common carcass weight. One alternative is to adjust individuals of each genetic group to their own mean for the covariate whenever the covariate is really a part of the performance comparison desired. Another alternative is to not adjust for variables which are part of the genetic trait evaluated (e.g., in lactation length from calf loss or illness under adverse environment, Madalena et al., 1989).

Editing of Data.

Experimental data should be carefully edited to detect erroneous observations before the data are analyzed, because such errors can very seriously bias the results and their interpretation. One approach in editing data is to identify observations that are more than about three standard deviations above or below the general mean for each trait measured. Suspect observations can then be rechecked for reasonableness. Observations for some traits can be checked systematically for consistency by examining their relationship to other traits of the same animal. For example, observations on weights at birth, weaning and marketing can be compared with rates of daily gain pre- and post-weaning and lengths of the pre-and post-weaning periods. Dates of death can be compared with dates of recorded weights or other observations.

Detection of errors in pedigree is especially important in genetic analyses, e.g., by checking pen assignments of sires and dams at breeding, dates of mortality and parturition of breeding females, etc. However, there is no complete substitute for care at the time data are first recorded. Unreasonable observations are best detected at the source, and rechecked at that time.

Evaluation of Net Production Efficiency.

The most useful economic criterion for choices among breeds or breeding systems is net production efficiency. As discussed earlier, effects on total cost per unit of output value are the ultimate basis for comparing systems of breeding or breeds for a given breed role in a specified breeding system and production environment.

If prior production system analysis has already provided a satisfactory basis for weighting component traits to predict effects of the chosen breed role on net efficiency of the production systems, choices among breeds and breeding systems are simplified. For example, see Tess et al. (1983b) and Bennett et al. (1983) for swine, Wang and Dickerson (1991) for sheep, and Núñez-Dominguez et al. (1992) for beef cattle. However, if such analyses of production systems have not been made, they become an essential part of the final interpretation of breed evaluation information.

Essential components of input costs to be predicted are the feed intakes required for breeding female maintenance, reproduction and product synthesis, and for maintenance and growth of progeny to market weight. If direct measures of feed intake are not possible, intake can be estimated from female measures of body weight, reproduction and product output (e.g., milk, wool, eggs) and progeny rate and composition of growth, as discussed ' earlier. Non-feed input costs for land, housing, labour, health maintenance and capital investment require management studies of the production system.

Output volume and value are generally measured more easily in terms of weights and composition of the animal products and of their values per unit based on studies of the range of market prices in the expected production-marketing systems, see Green et al. (1991) and Núñez-Dominguez et al. (1992) for examples in beef cattle.

Comparisons of breeds for a given breed role and the costs and prices of the input/output production system should be based on the optimum equilibrium age composition for each, including any significant differences in the timing of discounted expenses *vs* revenues within a year. If sufficient information is available on the changes in output to be expected with altered input or environments, rankings can be generalized, including effects for ranges of prices for both inputs and outputs (Melton et al., 1979;. Melton and Colette, 1992). When comparisons of breeding systems are based on annual input costs and output values for populations at optimum age equilibrium, differences in timing of expense and income seem unlikely to have important effects on efficiency rankings.

Germ Plasm Evaluation Programmes

The presumed purpose of animal evaluation programmes is to provide accurate and relevant information about the usefulness of alternative breeding stocks and breeding systems for defined breed roles and production-marketing environments. The two levels of animal germplasm evaluation programmes to be considered here are 1) Direct comparisons of genetic stocks and 2) Crossbreeding experiments. Programmes for genetic evaluation of individuals within breeds are considered only as they may contribute to comparisons among breeds.

General.

Direct comparisons of genetic stocks include a wide range of usefulness, from only growth efficiency of young males to total input/output efficiency of herds or flocks. Usefulness depends on both accuracy and completeness of information obtained. Accuracy is affected by method of sampling the stocks and by the design and scale of performance recording. Inaccurate or incomplete descriptive data can be not only inadequate but even misleading to those using the information to guide choice of breeding stock for a commercial animal production system. Crossbreeding experiments are planned matings to estimate not only mean performance differences among straightbred animals of different breeds or strains of livestock, but also to measure the parameters of breed, heterosis and gene-recombination effects in crosses that will allow prediction of relative efficiency for alternative breeds and systems of breeding. Examples of these two levels of germplasm evaluation programmes will be discussed for major species of livestock.

Poultry.

The "on farm" improvement and record of performance plans are useful primarily for selection within a breeder's own flocks. Both the possible selection of birds enrolled and environmental differences among breeders flocks limit the usefulness of published records for comparisons among genetic stocks. The early publicly operated central tests compared performance for samples of adult birds from different stocks under a common environment (Warren, 1958). However, the weaknesses of small and selected samples from each stock soon led to development of so-called Random Sample Performance Tests (Dickerson 1965). The avowed purpose of Random Sample Tests has been "to provide a reliable guide for commercial producers, hatcheries and breeders concerning the potential performance of commercial chicks or poults offered for sale by hatchery outlets".

For egg production stocks, random samples are obtained from commercial hatchery sources, preferably as hatching eggs rather than chicks. Performance is compared under a commercial egg production environment. Pens of each entry are replicated within a test location. Preferably, each stock is entered in a large number of different test locations, thereby increasing the reliability of the stock rankings based on data from all locations. Records of mortality, age at onset of lay, body size, egg production, egg size, shell strength, blood and meat spots and albumen quality are used to calculate egg and meat output value from each entry. Records of feed consumption and chick cost constitute input. Economic comparisons are made in terms of income over feed and chick cost per pullet housed (net income).

Feed per unit weight of eggs produced provides a measure of biological efficiency, but one which ignores output of salvage chicken meat at the end of the laying period. A measure of economic efficiency influenced less by stock differences in body size would be total input cost per unit of output value.

Two-year combined summaries of results from all Random Sample Egg Production Tests in U.S.A. and Canada provided overall estimates of breeding values, with 5% confidence limits, for each performance trait of each stock (e.g., see ARS, 1966). Information also was included for each trait concerning the average within-test correlation of the same stocks among replicates and between years, as well as the repeatability of the same stock between test locations in the same and different years. Because measures of some traits are much more accurate than others as indicators of their breeding values (i.e., more highly heritable), an index weighting of component traits was shown to be a better predictor of net income in future tests and years than net income itself (Kinney et al., 1969). This analysis also showed that future net income could be predicted nearly as accurately without including the measures of feed intake, using only age at first egg, eggs per hen housed, egg weights, laying mortality and hen body weight. Use of the same unselected control stock at all test locations over years permitted estimation of genetic changes over time for the genetic stocks entered in the tests.

Such analysis of test results helps users to realize the limited accuracy of results from a single year and test location (e.g., repeatability of .4 to .5 for net income) and the value of entering each stock at many test locations each year. However, even estimates of net income based on entries at many locations are far from perfectly accurate (e.g., $1.93 ± .10 per pullet housed for a stock with 80 pens at 32 locations). Even this accuracy is low enough that small changes in overall ranking of a stock can occur unpredictably from year to year, and is a reason for breeders to avoid relying too heavily on results of Random Sample Tests for their sales promotion.

In Random Sample Tests of chicken and turkey meat production stocks, maternal effects of parent flock health, age and egg size on chick size, mortality and later broiler weights make unbiased sampling of eggs for each entry difficult (Goodwin, 1961). Ideally samples for each stock entered should come from several parent-stock flocks of the same standard age. Primary emphasis has been placed on feed conversion or feed intake per unit weight of market birds. This measure ignores any differences in dressing percentage, or carcass composition, and in cost of chicks or poults, as affected by parent flock body size, egg production, fertility and hatchability of eggs. Factors affecting cost of broiler chicks or turkey poults presumably should be reflected in their price to growers. Evaluation of carcasses is increasingly important but more difficult, requiring direct or indirect measures of body fat and scores for conformation.

Random sample testing of poultry stocks can be useful both to the industry and to breeders, especially when there are many stocks to be compared and many independent growers. Properly conducted, such public evaluations of the available stocks direct industry attention to the real merit of the alternative breeding stocks. However, continued usefulness of such public testing to the poultry industry depends upon the accuracy and relevance of test information not obtainable more directly by individual producers and breeders.

At an earlier period, there were many breeds of both egg, meat and dual purpose chickens. Since then, there has been much Random Sample Testing and experimental evaluation of breeds and their crosses, leading to development of the present specialized egg and meat production stocks (Warren, 1942, 1958). In the meat stocks, specialized maternal and terminal sire lines have been developed to maximize efficiency in production of market meat birds. Parallel developments have occurred in meat turkeys. The extremely high reproductive rate of poultry, the intensive mass-production management systems and the intense competition in the poultry, egg and meat industry, have now led to sharply reduced numbers of surviving breeders in much of the world. Strain-crosses of Leghorn or part Leghorn composites have become the dominant egg producing stocks. Strain-crosses, with white feathers and skin for market acceptance, now dominate the chicken and turkey meat industry.

Diallel or partial diallel designs (Table 1) are generally used in crossbreeding evaluation of poultry breeds or strains (see review by Jacobec et al., 1987) because of their high reproductive rate and intensive management. Generally, first cross-heterosis is important for sexual maturity, rate of lay, viability and total egg mass per pullet housed. However, experiments extended to include F_2 or later generation progeny from inter se mating within the

F_1 cross have shown more loss of F_1 heterosis than the 50% expected from the reduced heterozygosity in the F_2 generation (review by Sheridan, 1981). This experience, and the very small proportion of pure line populations necessary to produce the parents of commercial chicks, logically have led to use of specific crosses by commercial producers. If composite lines are developed, it is done to obtain a desired blend of characteristics in a new line intended for later use as the male or female parent in some specific F_1 commercial cross.

Pigs.

Organized central performance testing of swine stocks began in Denmark in the early 1900's (Clausen and Gerwig, 1958). Typically, four slaughter pigs from each litter entered were fed together under standard conditions from about 20 to 90 kg to measure rate of gain, feed conversion and carcass traits. The purpose was to improve accuracy in comparing the genetic merit of breeder stock by testing all samples under a single uniform environment. This approach largely removed herd environmental differences from the comparisons and facilitated the uniform recording of feed consumption and of carcass traits. It also permitted valuable analyses of genetic variation in performance traits (Lush, 1936). However, the limited total capacity of the central testing facilities allowed only small and potentially selected (unrepresentative) samples of each breeder's stock for use as a sib or progeny test.

Similar central testing of samples from breeders spread to the U.S.A. and other countries in the 1920's (Craft, 1958). Then in the 1950's, testing samples of full or half-sib sets of boars alone, or of boars and sib-sets of barrows and gilts for slaughter was initiated in many states of U.S.A. and other countries (King, 1955). Boars with the better records are offered for sale to breeders. Such programmes allow comparison between boars from different breeders or even breeds, but the limited proportion of all boars that can be accommodated limits their accuracy in estimating differences among breeds or breeders. It also means that most selection by breeders still must be based on their own records.

A more complete central testing procedure was developed in Britain (MLC, 1977) and the Netherlands (Schoonoord, 1981) to compare commercial cross combinations offered by large breeders or breeding companies, using entries of both boars and gilts to measure whole litter growing performance and carcass traits (MLC, 1977). In Denmark (Jonsson, 1975), facilities have been expanded to allow growth and carcass testing of a set of four litter mates at one of twenty testing stations from each of one-half of all approved breeding sows. Participating breeders also record measures of age, weight and ultra-sonic sidefat, eye-muscle and fat areas. Thus breeders and producers have rather adequate summaries of both central test and on farm records to use in selecting replacement breeders and for choices among the breeds and breed crosses evaluated.

More recently "on-farm" recording of reproduction, growth and backfat performance in purebred herds of major US breeds (Stewart et al., 1991; Harris et al., 1989) has been organized to provide estimates of breeding values intended primarily for use in selection within breeds. However, such complete herd records are also highly useful for comparisons between breeds within a common regional production system. The main limitation of such comparisons is the lack of direct feed conversion records and incomplete carcass evaluation. These limitations can be overcome by joint use of the more limited central-test comparisons along with predictions from the "on-farm" body weights and backfat measures on live animals. The New Zealand Voluntary Improvement Plan (VIP, 1979) is an example of central boar testing combined with comprehensive on-farm performance recording. Clearly, the information necessary to characterize differences among pure breeds of swine can be obtained from both central test and on farm recording of performance or a combination of these approaches. Central testing can provide more complete information, but usually is handicapped by problems of cost and of small, potentially selected, samples. Error in breed comparisons from environmental variation among herds in on-farm performance recording can be largely overcome by averaging unselected records from many herds and very large numbers for each breed within a region. However, the primary focus of "on-farm" recording must be its use for within-herd selection, to avoid potential errors from environmental competition among herds.

The important improvements in viability and growth of market pigs and in productivity of sows from crossing pure breeds have been demonstrated in extensive crossbreeding experiments beginning in the early 1900's (Winters et al., 1937; Lush et al., 1939; reviews by Jonsson, 1975; Sellier, 1976; Johnson. 1981). Complete or partial diallel mating designs have been used, including three-way crosses to measure breed and heterosis effects on reproductive performance of the F, crossbred sows (as in Table 2). Some of these experiments also have compared F_1 with purebred boars of the same breeds and found significant heterosis in F_1 male reproductive performance, but negligible effects on performance of progeny.

Generally, crossbreeding results have indicated that maximum industry efficiency in pork production can be realized by mating females of an F_1, cross chosen for superiority in reproductive, growth and carcass traits with boars of the breed or F_1, cross with best transmitted viability, growth, carcass traits and superior male reproductive performance (Bennett et al., 1983). If deviations of heterosis from degree of heterozygosity are not importantly negative, composites of 3 or 4 maternal breeds or irregular "periodic" rotations of sire breeds would retain 2/3 to 3/4 of the average F_1 heterosis without requiring continued F_1 replacements from purebred populations (Dickerson, 1973; Bennett, 1987).

A design that would be useful in evaluating optimum fraction of an introduced breed in a composite (e.g., Young, 1991) is comparison of reciprocal backcrosses (1/4 *vs* 3/4 or 1/8 *vs* 7/8) relative to a common control and the F_2. Here backcross comparisons can be made within the same level of retained heterozygosity (Table 4).

A recent experiment (Young et al., 1989) has compared parental, F_1, F_2 and F_3 generations of crosses among two sets of four breeds each, chosen either for market pig traits or for sow performance and pig traits, to see how well F_3 composite performance agrees with prediction from parental and F_1 performance. The F_3 of the maternal breed cross was above prediction for number weaned, but later in puberty and lower in loin eye area. The F_3 of the paternal breed crosses was slightly above prediction for pig weight at weaning, earlier in puberty but lower in loin eye area. These minor deviations of performance from predictions based on only additive and dominant gene effects, along with the very small proportion of purebred matings required to produce replacements, have encouraged swine industry use of specific crossbreeding systems based upon estimates of the breed-average and F_1 heterosis effects for pig and sow performance traits.

Sheep and Goats.

Evaluation of sheep and goat germplasm covers a broad spectrum, from summaries of on-farm or field performance records to central testing of breed samples, to designed crossbreeding experiments measuring average breed heterosis, and non-allelic gene interaction effects. Performance traits studied vary with the major objective (meat, wool and/or milk) and with the production environment (temperate, tropical, intensive, extensive).

Organized on-farm field recording of information on unselected animals for reproductive rate, mortality, body weights and wool yields can provide initial characterization of differences among breeds maintained under similar regional management conditions. Of course, large total numbers are required to reduce the errors from environmental variation among the flocks sampled from each breed. More precise breed comparisons of growth rate, feed conversion, carcass composition, wool yield and quality, as well as milk production can be obtained by comparing samples from each pure breed under a uniform central test environment, provided that adequate numbers of representative samples are obtained from each breed (Turner, 1969). Central tests have been widely used to compare only the growth potential of rams from terminal sire breeds (Waldron et al., 1989), as a means of identifying the better sources of replacement rams. Addition of feed consumption records would increase the value of such ram testing. Central tests also could be used to compare sire progenies from several meat breeds for growth, feed conversion and carcass characters of ewe and wether lambs. Usefulness of such central test comparisons of breeds and breeders is heavily dependent upon adequate and representative sampling.

Experimental comparison of breeds for maternal (ewe) performance in market lamb production can be done most efficiently by mating representative ewes of each candidate breed to the same rams of one or more meat-type breeds. This experimental design minimizes sampling error from random sire effects on progeny in direct comparison of ewe breeds (e.g., Fimland et al., 1969).

When adequate numbers of ewes from the candidate breed are not available, representative rams of each maternal breed can be mated to ewes of one or more "native" breeds to produce the F_1 females, which, in turn are evaluated in subsequent matings with sires of the meat-type breeds (e.g., Jacobec and Drizik, in EEAP, 1988). This indirect design is approximately one-fourth as efficient because it measures only one-half of the maternal breed differences (Figure 1). However, there is no difference in the efficiency of comparisons among the meat-type sire breeds. Records needed for a comprehensive evaluation include not only those of ewe lifetime reproductive performance but also the viability, growth and carcass traits of the market lambs produced (Dickerson, 1977).

When the objective is to determine the optimum proportion of an exotic breed in composite populations derived from crossing with adapted native breeds, a mating design comparing ewes of the F_2 (i.e., from F_1 x F_1) generation with those of the 1/4 and 3/4 exotic backcrosses (as in Oltenacu et al., 1981) is efficient, because the proportion of maximum F_1, heterosis retained is expected to be equal (50%) for these three levels of exotic breed contribution (Table 4). A prime example is the worldwide experimental evaluation of Finnsheep and other prolific breeds to increase net productivity under environments ranging from temperate to subtropical and from intensive to extensive range management (EEAP, 1988). Some of these experiments compared F_1, with the less heterozygous backcrosses, but the estimated fractional breed effects for litter size born were relatively unbiased because heterosis was slight. A Canadian experiment compared levels from 1/8 to 7/8 and purebred Finnsheep ewes (Fahmy, 1990). The reviews by Baker and others in an EEAP symposium (EEAP, 1988) provide a comprehensive summary of experiments evaluating potential usefulness of Finnsheep crossbreeding under diverse managements. Experiments comparing Finnsheep with Romanov, Booroola and other prolific breeds also are discussed.

Choices between systematic crossbreeding and the optimum composite require estimates of the average heterosis in overall performance realized for the two systems, including the dilution of average heterosis from the proportion of purebreds required to sustain each system. Such a comparison requires prediction of performance and over-all efficiency for the complete crossbreeding system, and for the F_2 or later generation of the inter se mated composite, using deviations from weighted means for the pure breeds involved, as in Young et al. (1986). For meat production in sheep, comparisons likely would include maternal composite or maternal crossbred ewes, when both are mated to meat-breed rams, and a straightbred general-purpose composite. Such comparisons should include all important traits and the relative values of wool and lamb that influence lifetime ewe productivity under the intended production-marketing system (Ercanbrack and Knight, 1989). Breed differences for each breed role in crossbreeding could be based on input costs per unit of output value in the experiment and compared with expected breed differences in unit costs based on prior estimates of the economic weightings for each trait (e.g., Wang et. al., 1991).

Because of the large differences among sheep breeds in prolificacy *vs* growth-carcass merit, industry breeding systems for market lamb production generally use superior large growth-carcass breeds to sire lambs from ewes of smaller, more prolific breeds, breed-crosses or composites. Choice of the ewe-breeds depends partly upon the feasability of production environments in which nutrition, matings and care at lambing can be controlled. Heterosis retained in prolific part-Finnsheep composites (Young et al., 1986) has been encouraging for their use in crossing with terminal sire breeds, thus simplifying matings required for production of replacement ewes. However, there has been considerable variation among sheep crossbreeding experiments from linear association of heterosis retained with level of increased heterozygosity expected, possibly related to interaction with production environments. Thus experimental evaluation of promising composite breed combinations seems justified before recommending their adaption for industry use.

Beef Cattle.

The various types of on-farm "record of performance" programmes are intended primarily for use in selection within a pure breed (Gregory et al., 1961). However, when averaged across many herds of each breed, they can provide much useful information about differences among breeds that exist within the same geographical and livestock management region. Their value depends on accurate measurement and reporting of the important performance traits for unselected animals. It is not usually feasible to include on-farm records of feed consumption or of carcass composition. Central Testing Stations can be used to compare samples from different breeds under a common environment for some of the important performance traits, such as growth, feed conversion, conformation and live fat measures of young bulls (Olson, 1989) or these traits plus carcass traits of steers. However, the small number of potentially selected animals and traits measured tend to limit both the accuracy and completeness of breed comparisons based on information from Central Tests.

The major potential advantages of planned beef cattle crossbreeding experiments are 1) the measurement of both breed average and crossbreeding heterosis effects, 2) minimizing environmental sources of error and 3) more complete measurement of traits affecting production efficiency. The production objective may be meat production only or a combination of meat and milk production. In some cases, it may be desirable to include more than one environment or management system in the experiment, although this multiplies the necessary scale of the experiment (e.g., Olson et al., 1991).

When the objective is to evaluate several introduced or exotic breeds, the more feasible crossbreeding design is one comparing a representative sample of sires from each introduced breed in matings with one or more "native" breeds to improve performance potential or adaptation to a difficult environment (Figure 1, Table 4 as in Gregory et al., 1985; Trail et al., 1985, or Paschal et al., 1991). The first generation allows comparison among introduced breeds for the combination of transmitted (g^I) and heterosis (h^I) effects of each breed of sire. Adding information from the F_2 and the two backcross generation matings would allow separate estimation of breed differences in transmitted individual (g^I), heterosis (h^I), and recombination effects (r^I). It also would allow evaluation of the optimum fraction of each introduced breed from 1/4 to 3/4 at the same proportion of F_1 increase in heterozygosity (Table 4).

Estimation of maternal breed (g^M), heterosis (h^M) and recombination (r^M) effects requires third generation matings of generation-two females with sires of an unrelated breed (Table 4), and combining these results with information from generations one and two. See Cundiff et al., (1986) and references cited for partial examples of this approach. A summary of information from these breed and crossbreeding evaluation experiments, as applied to the choices among alternative crossbreeding systems, is given by Gregory and Cundiff (1980).

When adequate samples of females as well as males are available from each breed to be evaluated, the complete diallel design (Table 1, as in Gregory et al., 1980; Baker et al., 1989; or Comerford et al., 1991) is more efficient for estimating breed individual (g^I) and maternal (g^M) and individual heterosis (h^I) effects. It can be extended to measure maternal heterosis (h^M) by including the three-way crosses (Table 2). However, measurement of individual recombination effect (r^I) deviations from linear association with average changes in heterozygosity (i.e., from the additive plus dominance expectations) would require comparison of F_2 with mean of reciprocal backcrosses (Table 4).

Possible non-allelic gene interaction deviations from linear association with expected heterozygosity (r^I, r^M, r^p) could be measured most completely by comparing deviations from purebred means for each four-way cross with those for the mean of the corresponding four F_3 generation two-way crosses (Table 3). If paternal effects (g^p, h^p, r^p) are negligible, similar comparisons for each three-way cross with those for the mean F_3 generation of the two corresponding two-way crosses (Table 3) would provide similar estimates for r^I and r^M deviations, e.g.,

$$\frac{1}{4}(CA^3+CB^3+DA^3+DB^3-C-D-A-B)-\frac{1}{2}(CDxAB)+\frac{1}{8}(C+D+A+B)$$

$$=\frac{1}{8}r^I_{gg}+\frac{1}{4}(r^I_{dd}+r^M_{gg})+\frac{1}{2}r^M_{dd}\text{, and}$$

$$\frac{1}{2}(CA^3+CB^3)-\frac{C}{2}-\frac{A}{4}-\frac{B}{4}-\frac{1}{2}(CxAB)+\frac{C}{4}+\frac{A}{8}+\frac{B}{8}$$

$$=\frac{3}{16}r^I_{gg}+\frac{3}{8}r^I_{dd}+\frac{1}{4}r^M_{gg}+\frac{1}{2}r^M_{dd}$$

Several large scale studies of heterosis retention in beef cattle (Gregory and Cundiff, 1980; Koch et al., 1985; Gregory et al., 1991a,b) under favorable temperate environments have not detected important deviations from additive-dominance expectations in advanced generations of composite populations. If these results are representative of cattle in general, most breed and crossbreeding evaluation studies need not extend beyond the three-way crosses needed to evaluate heterosis in maternal performance. However, crossbreeding results with dairy cattle (Madalena, 1989; Madalena et al., 1990a) have indicated important recombination losses in composites under difficult tropical environments.

Dairy Cattle.

The trait of primary importance in dairy cattle obviously is milk production, qualified by fat, protein and total solids content. However, efficiency of milk production can be also greatly affected by fertility, mortality and culling as they affect herd life and replacement costs, as well as by fixed and maintenance costs related to health care and cow size (Blake et al., 1986a; Schmidt and Pritchard, 1988, Holman et al., 1990). Resistance to disease and parasites and the tolerance of heat and of marginal feed intake are especially important under some tropical, low-input production systems. Adjustments should be avoided for such gene-influenced components of milk production as age at first calving or lactation length under stressful environments (Madalena et al., 1989).

Within-herd recording of milk, fat and now protein production is the longest, most systematic and best utilized system of performance recording for domestic animals. Although the DHIA system of performance recording is intended for use in within-breed selection, breed averages across herds under similar management clearly are good measures of breed differences in performance, and can be used for comparing genetic evaluations between countries as well (Philipsson, 1987). Within-herd records of milk, fat and protein production, supplemented by body weights and reproductive performance of pedigreed cattle could even be used to estimate breed differences in the economic efficiency of milk production, under ranges of relative prices for milk components, feedstuffs and other inputs (Blake et al., 1986a; Schmidt and Pritchard, 1988). Properly controlled, such field comparisons could even be used to compare breeds of dairy cattle with crosses between breeds (Fimland, 1975; Ericson, 1987; Ahlborn-Bruer and Hohenboken, 1991). Thus, designed breed evaluation experiments are needed mainly for the comprehensive evaluation of breeds in crossbreeding, including crossing of native with exotic breeds to improve performance in difficult environments (Simpson and Wilcox, 1982; Blake et al., 1986b; Cunningham and Syrstad, 1987; Syrstad, 1988; Cunningham, 1989; Tewolde et al., 1990).

The most informative crossing design is a complete diallel extended to include the three-way crosses of females from each F_1 and contemporary purebreds by the same sires (Tables 1 and 2). The USDA diallel crossing of Holstein, Ayrshire and Swiss breeds (McDowell and McDaniel, 1968) included these matings plus the first generation of a three-breed rotation. Heterosis for fat corrected milk production was 8 to 10% in F_1 crosses with Ayrshire and Brown Swiss but negligible for Ayrshire x Swiss F_1. Heterosis in milk yield was even greater for the three-way crosses. However, only the Ayrshire x Holstein, Swiss x Holstein and Holstein x (Ayrshire - Swiss) exceeded purebred Holstein in first lactation net return, after adjusting for differences in health, mortality and calving interval.

The Holstein x Guernsey crossbreeding experiment at the University of Illinois (Touchberry, 1970, 1992) attempted to include all outputs and inputs affecting efficiency of dairy production (e.g., milk solids yield, viability, reproduction, body weights, veterinary service, mastitis, etc.). Breeding groups compared were purebred Holstein and Guernsey, and reciprocal F_1 crosses, from the same sire within a year and the same dams in different years. The second generation compared the two pure breeds with 1/4 and 3/4 Holstein backcrosses, using the same Holstein or Guernsey bulls to sire each pair of purebred and backcross progenies and allowing each F_1 female to be mated for both backcrosses in different years. The third generation included the two pure breeds plus the 3/8 and 5/8 backcrosses, from matings of the same sires to produce either pure and 5/8 Holstein or pure and 5/8 Guernsey progeny. The next two generations were from crisscross matings of Holstein sires with pure and 3/8 Holstein and Guernsey sires with pure and 3/8 Guernsey females followed by the reverse backcross, to produce 5/16, 11/16, 11/32 and 21/36 and 100% Holstein and Guernsey progeny, approaching the equilibrium 1/3 to 2/3 of a two-breed rotation. Effects of breed additive and crossbreeding heterozygosity were estimated from partial regressions on fractional breed of sire or dam and heterozygosity. The F_1 heterosis was about 7% for total milk solids, but nearer 22% in terms of net return after adjustment for reproductive, health and other traits. However, the pure Holsteins used still exceeded the F_1 crosses by about 10%, because the pure Holsteins exceeded Guernsey's used by over 100% in estimated income over input costs. Thus, the potential advantage from crossbreeding would be much greater between breeds of more nearly equivalent performance, as for Jerseys and Holsteins under the seasonal-pasture, milk-solids production system of New Zealand (Ahlborn-Breur and Hohenboken, 1991). There, Jersey-Holstein rotation crossbreeding apparently would slightly exceed pure Holstein fat production before taking into account crossbred advantages in reproduction, viability, and other performance.

Because of the general superiority of the Holstein-Friesian breed for milk production, especially in temperate climates, interest has focussed on differences among Friesian strains from different countries. The FAO sponsored comparison in Poland of 10 strains of Friesian cattle (Stolzman et al., 1988; Jasiorowski et al., 1988a,b) compared the F_1 and the 3/4 and 1/4 backcrosses of nine other strains with Polish Friesian. Differences among the nine F_1 crosses with the Polish Friesians would include $1/2\ g^I + h^I$ effects for each strain. Those among the nine breed of sire 3/4 backcrosses would contain $3/4\ g^I + 1/2\ h^I + 1/8\ r^I + 1/2\ g^M + h^M$ effects for each strain. Comparisons of 3/4 with 1/4 backcrosses would contain only the $1/2\ g^I$ effect of each strain, and this would indirectly permit estimation of differences in h^I from the combination of F_1 and backcross information. Use of estimates for g^I and h^I differences between strains would then permit estimates of differences in $1/2\ g^M + h^M + 1/8\ r^I$. If contemporary purebred Polish Friesians had been included, the experiment would have been much more efficient for estimating both individual and maternal heterosis (h^I and h^M). Inclusion of the F_2 generation of each cross would have allowed estimation of epistatic recombination effects as well (Table 4).

Another important question concerns the role of high producing dairy breeds from temperate climates in the crossbreeding improvement of milk production in more difficult tropical environments (Simpson and Wilcox, 1982; Cunningham and Syrstad, 1987a; Cunningham, 1989; Tewolde et al., 1990) or role of Zebu cattle crossbreeding in semitropical environments (Blake et al., 1986b). This question can be approached from analysis of well planned experiments on cooperator farms as in Madalena et al. (1989; 1990a), being careful to avoid adjustment for gene-influenced components of milk production, such as lactation length and age at first calving. Partial regressions on fractions for breed composition and on relative crossbreeding increase in heterozygosity (Robison et al., 1981) can be used. When inter se matings of crossbreds are included along with levels of backcrossing to both exotic and adapted native breeds (as in Madalena et al., 1989; 1990a), epistatic recombination deviations from additive breed and dominance effects can be detected (Table 3). For example, performance of the 5/8 inter se in this analysis was markedly below the additive plus dominance expectations, relative to those for the 1/4 to 31/32 Holstein crosses with Guzera. Madalena et al. (1990b) also compared profit/day of herd life for the F_1, 3/4 Holstein, 5/8 inter se, rotational cross and modified 2 Holstein: 1 Guzera rotation, under high and low management levels. Results emphasized the greater advantage of F_1 over 3/4 Holstein for low than for high management. Also results from the 2 Holstein: 1 Guzera (2H:1G) rotation relative to F_1 were good (75%) under high management, while the 1H:1G rotation was 60% of F_1 and better than the 2H:1G rotation under low management. However, Syrstad's (1990) summary analysis of many studies comparing F_1 and 3/4 backcross milk yields of first parity Holstein and Jersey crosses indicated that the increased exotic breed effect at least compensated for the reduced heterozygosity of the 3/4 backcross over a wide range of herd production levels. Also, the ratio of Jersey to Holstein F_I, crosses was similar from low to high herd production levels. Perhaps, more evidence for interaction of heterosis or breed effects with herd production level would have been detected if viability, lactation length and age at first calving could have been examined.

These results suggest caution in assuming linear association of heterosis with heterozygosity retained in breed composite populations until further experimental evidence is obtained for the full array of important component traits, especially under difficult production environments.

Summary

The assumed purpose of breed and crossbreeding evaluation efforts is to allow and encourage optimum use of animal germplasm to improve efficiency of livestock production under the many diverse world production-marketing environments. This requires clear definition of production efficiency and of the effects of alternative genetic changes in performance traits on both output value and input cost under defined production-marketing systems. Prediction of optimum breed use in production systems (ranging from pure breeds to specific or rotation crossbreeding to formation of new composite breeds) requires knowledge of breed differences and crossbreeding heterosis and of any important deviations from expectations for only average and dominant gene effects. This information should include individual, maternal and possible paternal effects on such traits as reproduction, viability, growth, body composition and female production of milk, wool or eggs, and how these are affected by environmental differences. Experimental approaches for obtaining the needed estimates of breed and crossbreeding parameters are described, with examples from the major classes of livestock. In poultry and swine, central tests can be used to characterize available commercial stocks, but designed crossing experiments are needed to fully estimate the parameters required to predict the optimum choices of breeds and system of breeding. In some ruminant species, and especially in dairy cattle, much of the needed information on breed, heterosis and even deviations of interse mated crossbred populations from additive dominance expectations, can be obtained from well planned field records on animals of known pedigree. However, more complete and critical evaluation of exotic breeds and their crosses with indigenous breeds can be accomplished in designed experiments, including the combination of either 1) indigenous breeds, F_1 reciprocal backcrosses, F_2, F_3, and for maternal heterosis, F_1 crosses with a common unrelated breed of sire, or 2) a diallel design, including reciprocal three-breed crosses to measure breed of female performance and maternal heterosis effects, with extension to matings of each set of F_1 and F_2 and two backcross females with a common breed of sire to measure effect of exotic breed fraction, independent of heterosis, and any deviations from additive/dominance expectations. Experiments directly comparing multi-breed composites (F_3 + generations) with constituent breed crosses and parental purebreds provide the most complete evaluation for the role of composites relative to specific or rotation crossbreeding, when the required proportion of industry purebred matings is also considered.

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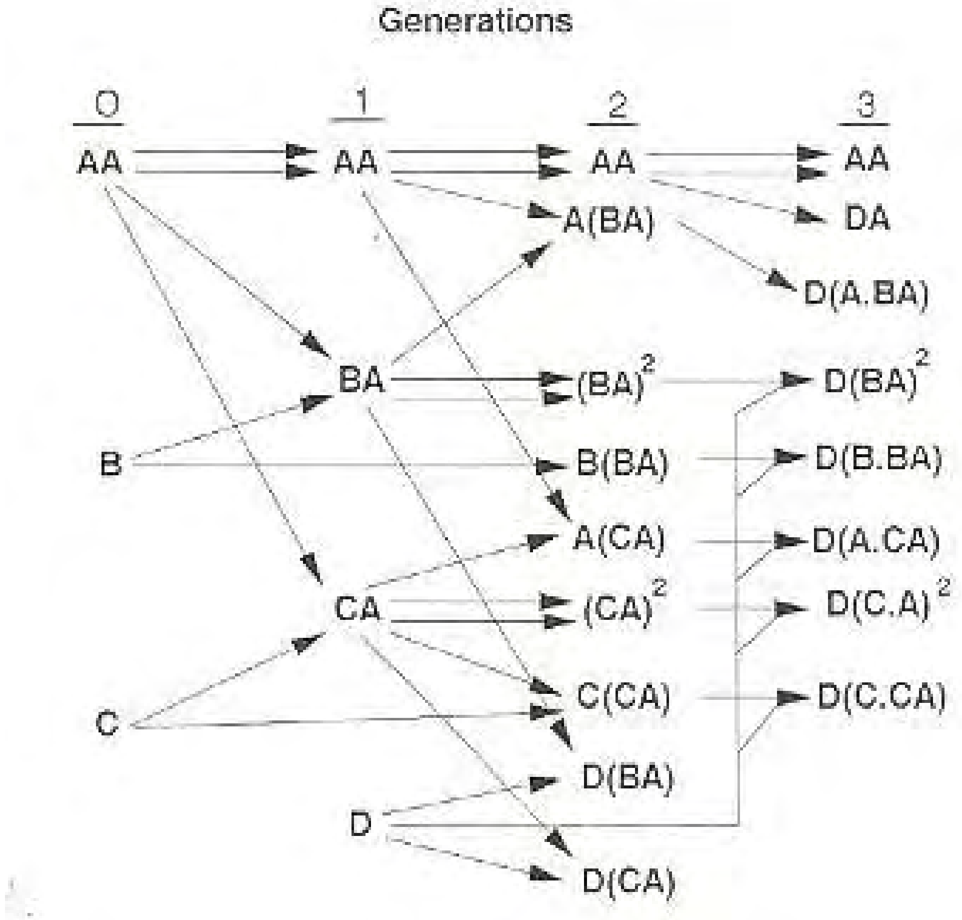

FIGURE 1. Mating plan for topcross, backcross and interse design for evaluating two exotic breeds (B and C) relative to an adapted native breed (A)

TABLE 1. Expectations for genetic effects in a diallel crossbreeeding system

Breed of sire (j)	Breed of dam (i)		
	A	B	C
A	g^I_A $g^P_A+g^M_A$ 0	$1/2(g^I_A+g^I_B)$ $g^P_A+g^M_B$ $\bar{h}^I_{AB}+s^I_{AB}$	$1/2(g^I_A+g^I_C)$ $g^P_A+g^M_C$ $\bar{h}^I_{AC}+s^I_{AC}$
B	$1/2(g^I_B+g^I_A)$ $g^P_B+g^M_A$ $\bar{h}_{AB}+s^I_{BA}$	g^I_B $g^P_B+g^M_B$ 0	$1/2(g^I_B+g^I_C)$ $g^P_B+g^M_C$ $\bar{h}^I_{BC}+s^I_{BC}$
C	$1/2(g^I_C+g^I_A)$ $g^P_C+g^M_A$ $\bar{h}^I_{AC}+s^I_{CA}$	$1/2(G^I_C+g^I_B)$ $g^P_C+g^M_B$ $\bar{h}^I_{BC}+s^I_{CB}$	g^I_C $g^P_C+g^M_C$ 0

where:

g^I_i and g^M_i are breed average individual and maternal effects, and $\sum g^I_i =$

$\sum g^M_i = 0$.

$\bar{h}_{ij}$, is the mean heterosis effect for a two-breed <u>reciprocal</u> cross

$\bar{P}_j$, is mean phenotype for one purebred $= \bar{P} + g^I_j + g^M_j$

X_{ij}, is mean phenotype for a two-breed-cross $= \bar{P}_n + 1/2(g^I_i + g^I_j) +$

$g^M_j + \bar{h}_{ij}$

$\hat{g}^M_j - g^P_j = \sum_1^{n-1}(X_{ij} - X_{ij})$SCALESYM100/n, = breed maternal less

paternal effect, because

$$(n-1)(g^M_j - g^P_j) - \sum_1^{n}(g^M_i - g^P_i) + (g^M_j - g^P_j) = n(g^M_j - g^P_j).$$

$\hat{g}^I_j = P_j - \bar{P}_n - \hat{g}^M_j$ = breed mean individual effect

$\bar{h}^I_{ij} = \frac{1}{2}(X_{ij} + X_{ji} - P_i - P_j) =$ mean heterosis for reciprocal cross.

$s^I_{ij} = \frac{1}{2}(X_{ij} - X_{ji}) - \frac{1}{2}(g^M_j - g^M_i) =$ specific reciprocal effect

$\bar{h}^I_i$ = breed mean heterosis $= \dfrac{\sum_I^{2(n-1)} X_{ij} - (n-1)P_i - \sum_I^{(n-1)} P_j}{2(n-1)} = \sum_I^{n-1} \bar{h}^I_{ij}$SCALESYM125/(n − 1)

Table 2. Second phase of diallel mating design to estimate heterosis for maternal effects on progeny performance (h^M)[a].

Breed of dams	Breed of sires			
	A	B	C	D
A		B •A	C•A	D•A
B	A•B		C •B	D•B
C	A•C	B •C		D•C
D	A•D	B •D	C •D	
AB+BA			C(AB+BA)	D(AB+BA)
AC+CA		B(AC+CA)		D(AC+CA)
AD+DA		B(AD+DA)	C(AD+DA)	
BC+CB	A(BC+CB)			D(BC+CB)
BD+DB	A(BD+DB)		C(BD+DB)	
CD+DC	A(CD+DC)	B(CD+DC)		

$h^M_{AB}+1/8r^I_{AB}$ = (C•AB+C•BA – C•A – C•B+D(AB)+D(BA) – D•A-D•B)/4

---

[a] Sampling error for estimates of $h^M_{ij}+1/8\ r^I_{ij}$ will be minimum, for any total scale of experiment, when equal numbers of contemporary progeny are produced for each mating combination, i.e. DA, DB, D(A•B) and D(B•A), and when each sire of a breed produces the same proportion of progeny in each cross.

Table 3. Expected fraction of defined genetic components in deviations of alternative crossbreeding categories from weighted mean of parental breeds relative to F_t heterosis, h = d + l/2gg.

	Heterosis			Recombination[b]							
generation[a]	h^I	h^M	h^P	r^I_{gg}	r^I_{dd}	r^M_{gg}	r^M_{dd}	r^P_{gg}	r^P_{dd}	g^M	g^P
$\overline{F}_1$	1	0	0	0	0	0	0	0	0	0	0
$\overline{F}_2$	1/2	1	1	1/4	1/2	0	0	0	0	0	0
$\overline{F}_3$	1/2	1/2	1/2	1/4	1/2	1/4	1/2	1/4	1/2	0	0
	1/2	1	0								
A(A•B)	SCALESYM32}			1/8	1/2	0	0	0	0	0	0
$\overline{B}_1$ B(A•B)	1/2	0	1								
AB×A											
AB×B	$1-\sum_1^n q_i^2$	——	>	$\frac{1}{2}-(1-\sum_1^n q_i^2)$	$1-\sum_1^n q_i^2$	$\frac{1}{2}(1-\sum_1^n q_i^2)$	$1-\sum_1^n q_i^2$	$\frac{1}{2}(1-\sum_1^n q_i^2)$	$1-\sum_1^n q_i^2$		
Composite											
n=2	1/2	1/2	1/2	1/4	1/2	1/4	1/2	1/4	1/2	0	0
n=3	2/3	2/3	2/3	1/3	2/3	1/3	2/3	1/3	2/3	0	0
n=4	3/4	3/4	3/4	3/8	3/4	3/8	3/4	3/8	3/4	0	0
Rotation	$(\frac{2^n-2}{2^n-1})$	——>	0	$\frac{1}{6}(\frac{2^n-2}{2^n-1})$	$\frac{2}{3}(\frac{2^n-2}{2^n-1})$	$\frac{1}{6}(\frac{2^n-2}{2^n-1})$	$\frac{2}{3}(\frac{2^n-2}{2^n-1})$	0	0		
n=2	2/3	——>	0	1/9	4/9	1/9	4/9	0	0	0	0
n=3	6/7	——>	0	1/7	4/7	1/7	4/7	0	0	0	0
n=4	14/15	——>	0	7/45	28/45	7/45	28/45	0	0	0	0
C♂ Rotation♀											
n=2	1	2/3	0	1/9	4/9	1/9	4/9	0	0	0	0
n=3	1	6/7	0	1/7	4/7	1/7	4/7	0	0	0	0
n=4	1	14/15	0	1/45	28/45	7/45	28/45	0	0	0	0
3-breed Cross											
C♂ × A • B♀	1	1	0	1/8	1/4	0	0	0		$\frac{A+B}{4}-\frac{C}{2}$	$\frac{C}{2}-\frac{(A+B)}{4}$
A • B♂ × C♀	1	0	1	1/8	1/4	0	0	0		$\frac{C}{2}-\frac{(A+B)}{4}$	$\frac{1}{4}(A+B)-\frac{C}{2}$
4 Breed Cross											
CD♂ × AB♀	1	1	1	1/4	1/2	0	0	0		$\frac{1}{4}(A+B-C-D)$	$\frac{1}{4}(C+D-A-B)$

[a] Mean of reciprocal crosses, equilibrium for n sire breed rotation, or for q_i, fractions of n breeds in a composite at F_3 or later generation.

[b] From Dickerson (1973) and Hill (1982).

Table 4. Expected fraction of defined genetic components in linear contrasts between means for alternative mating[a]

Code	Linear Contrast	g^I	h^I	r^I	g^M	h^M	r^M
1	BA–AA	(B–A)/2	BA	0	0	0	0
2	BA–CA	(B–C)/2	BA–CA	0	0	0	0
3	A(BA)–AA	(B–A)/4	BA/2	BA/8	(B–A)/2	BA	0
4	(BA)^2–AA	(B–A)/2	BA/2	BA/4	(B–A)/2	BA	0
5	B(BA)–AA	3(B–A)/4	BA/2	BA/8	(B–A)/2	BA	0
5–3		(B–A)/2	0	0	0	0	0
4–(3+5)/2		0	0	BA/8	0	0	0
6	A(BA)–A(CA)	(B–C)/4	(BA–CA)/2	(BA–CA)/8	(B–C)/2	BA–CA	0
7	(BA)^2–(CA)^2	(B–C)/2	(BA–CA)/2	(BA–CA)/4	(B–C)/2	BA–CA	0
8	B(BA)–C(CA)	3(B–C)/4	(BA–CA)/2	(BA–CA)/8	(B–C)/2	BA–CA	0
8–6		(B–C)/2	0	0	0	0	0
7–(8+6)/2		0	0	(BA–CA)/8	0	0	0
9	D(BA)–AA	$\frac{D}{2}+\frac{B}{4}-\frac{3}{4}A$	(DB+DA)/2	BA/8	(B–A)/2	BA	0
10	D(A·BA)–AA	$\frac{D}{2}+\frac{B}{8}-\frac{5}{8}A$	$\frac{DB}{4}+\frac{3}{4}DA$	3BA/32	(B–A)/4	BA/2	BA/8
11	D(BA)^2–AA	$\frac{D}{2}+\frac{B}{4}-\frac{3}{4}A$	(DB+DA)/2	4BA/32	(B–A)/2	BA/2	BA/4
12	D(B·BA)–AA	$\frac{D}{2}+\frac{3B}{8}-\frac{7}{8}A$	$\frac{D}{2}DB+\frac{DA}{4}$	3BA/32	3(B–A)/4	BA/2	BA/8
12–10		(B–A)/4	(DB–DA)/2	0	(B–A)/2	0	0
9–11		0	0	0	0	BA/2	–BA/4
13	D(BA–D(CA)	(B–C)/4	(DB–DC)/2	(BA–CA)/8	(B–C)/2	BA–CA	0
14	D(A·BA)–D(A·CA)	(B–C)/8	(DB–DC)/4	3(BA–CA)/32	(B–C)/4	(BA–CA)/2	(BA–CA)/8
15	D(BA)^2 $^-$D(CA)^2	(B–C)/4	(DB–DC)/2	(BA–CA)/8	(B–C)/2	(BA–CA)/2	(BA–CA)/4
16	D(B·BA)–D(C·CA)	3(B–C)/8	3(DB–DC)/4	3(BA–CA)/32	(B–C)/4	(BA–CA)/2	(BA–CA)/8
13–15		0	0	0	0	(BA–CA)/2	–(BA–CA)/4
15–(14+16)/2 11–(10+12)/2		0	0	(BA–CA)/32	0	0	(BA–CA)/8

[a]"Individual (I) and maternal (M) additive (g^I and g^M), heterosis h^I and h^M and non-allelic gene interaction (r^I and r^M) effects on performance traits.

Table 5. Level of significance (P) for a 5% mean difference (+ or -) between two strains in traits with differing Coefficient Variation (CV) and heritability (h^2).

No progeny per		No. sires /strain N_s	SE^a $(\bar{G}_1 - \bar{G}_2)$	$t = \frac{\bar{G}_1 - \bar{G}_2}{\mathrm{SE}}$	Minimum t for[c]	
strain n_G	sire n_{GS}				P_{05}	P_{01}
a. CV = 20%; h^2 = 10%						
280	28	10	1.95	2.57	2.10	2.88
	20	14	1.87	2.67	2.06	2.78
	14	20	1.81	2.76	2.02	2.71
	10	28	1.77	2.82	2.01	2.67
	5	56	1.72	2.90	1.98	2.62
220	20	11	2.11	2.37	2.09	2.85
	10	22	2.00	2.50	2.02	2.71
	5	44	1.94	2.57	1.99	2.63
b. CV = 10%; h^2 = 10%						
140	20	7	1.45	3.44	2.18	3.06
	10	14	1.32	3.78	2.06	2.78
	5	28	1.25	3.99	2.01	2.67
100	20	5	1.72	2.91	2.31	3.36
	10	10	1.56	3.20	2.10	2.88
	5	20	1.48	3.37	2.02	2.71
80	20	4	1.92	2.60	2.45	3.71
	10	8	1.75	2.85	2.14	2.98
	5	16	1.66	3.02	2.04	2.75
60	20	3	2.22	2.25	2.78	4.60
	10	6	2.02	2.47	2.23	3.17
	5	12	1.92	2.60	2.07	2.82
40	20	2	2.72	1.84	4.30	9.92
	10	4	2.48	2.02	2.45	3.71
	5	8	2.34	2.13	2.14	2.98

[a] $\%\mathrm{SE}(\bar{G}_1 - \bar{G}_2) = \sqrt{2(390/N_G + 10/N_S)}$ with $df = 2(N_s - 1)$. Total phenotypic variance are expressed as the squared coefficient of variation (%), assuming one (1) progeny per dam.

[b] $\%\mathrm{SE}(G_1 - G_2) = \sqrt{2(97.5/n_G + 2.5/N_s)}$

[c] See Table A.3 in Steele and Torrie (1960) or any other source of probability values for t-ratio, plus or minus mean difference (i.e. 2-tailed distributions).

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