Topics to be confronted in development of industry structures to facilitate and evaluate genetic change include the nature and extent of genotype by environment interactions (GEI), development of coherent procedures for simultaneous within- and across breed selection, the role of cooperative group breeding schemes, and the potential impact of elite nucleus herds propagated using advanced reproductive technologies. GEI can lead to subdivision of populations, but will more likely place a premium on use of multiple-trait analyses or testing in multiple herds to accommodate GEI involving fixed and random environments, respectively. Joint within- and across-breed selection requires information on breed and heterosis parameters, within-breed genetic evaluations and genetic trends and would be facilitated by greater use of crossbred data in national evaluation programs. Nucleus breeding schemes may accelerate rates of genetic improvement, but must accommodate retention of genetic variation sufficient to allow adaptation to changing environments and selection objectives.

INTRODUCTION

Management of genetic change in pastoral meat species requires joint application of quantitative and ecological genetic theory. Adaptation is a critical issue when animals harvest their own food by grazing over relatively large areas in diverse environments. The level of environmental control in commercial beef cattle and sheep holdings varies greatly among environments, and in part determines access to animals at different periods during the life cycle, thereby determining which data can be readily collected. Improved data collection practices often require that increased levels of environmental control be imposed in seedstock herds and flocks, but the applicability of such data to less well controlled conditions can then be questioned. Uniformity of environment, or at least the absence of genotype x environment interaction, thus becomes a critical consideration in definition of selection objectives for individual herds or flocks and in configuration of national programs for genetic evaluation of individuals and breeds. Industry structure likewise affects both the rate of improvement in seedstock herds and flocks and the dissemination of that genetic improvement into the commercial sector.

Certain articles of faith shape our view of applied sheep and beef cattle breeding. Most probably are essentially correct, but their implications should periodically be questioned, especially in view of rapidly evolving breeding value estimation procedures and reproductive technologies. First, the selection objective in grazing ruminants (Johnson and Garrick, 1990) is usually thought to be a multitrait, nonlinear function of genetic potentials. The selection objective (net merit) is presumed to be different in different environments and different populations. Variation in selection objective among environments often relates to the importance of traits involving environmental adaptation in definition of net merit, and which, in turn, is a reflection of degree of environmental control. Second, genotype x environment interactions (GEI) are considered widespread but can be considered at several levels, each
with important (but different) implications for the design of improvement programs. GEI for net merit clearly exist as a simple reflection of differences in selection objective among environments and populations. However, the importance of within-breed GEI (i.e., of animal × environment interactions) for components of net merit has not been clearly defined. Such interactions are presumed to exist, as a logical extension of identifiable breed and line by environment interactions, but consensus has not emerged on procedures for their evaluation and utilization in improvement programs.

Third, in much of the world, the lack of both vertical and horizontal integration in sheep and beef cattle enterprises limits opportunities for improvement. Herds and flocks in much of the world are small, with little opportunity for within-herd selection. This situation places a premium on use of artificial insemination (AI) to provide genetic ties among seedstock herds and thereby facilitate combined within- and among-herd selection. This opportunity has been partially realized in beef cattle but has not been effectively realized in sheep. In terms of vertical integration, sale of calves at weaning in much of North America often limits data collection in commercial herds to that available at weaning. Postweaning performance and carcass value must thus be inferred from traits observable at weaning, or selection must be based on data collected on intact males in seedstock herds. The level of vertical integration is usually greater in sheep than in beef cattle, although sale of lambs at weaning is common in many environments. In both species, provision for collection of carcass data has been out of the hands of most producers, despite periodic efforts to maintain identity of slaughter animals. Ultrasound technology may rectify this situation for traits associated with carcass leanness but cannot yet provide information on intramuscular fatness (marbling) which is critical in some markets.

Lastly, the assumption has been that the reproductive biology of cattle and sheep will necessitate slower rates of genetic change than those possible in pigs and poultry. Yet advances in superovulation and embryo transfer (Smith, 1986; Gearheart et al., 1989) could change that situation importantly, especially in elite seedstock herds.

**GENOTYPE-ENVIRONMENT INTERACTION (GEI)**

The net merit of individual animals, defined via the selection objective, is expected to differ among regions and herds. These differences necessarily lead to differences in rank among individuals and therefore to GEI for net merit. GEI for net merit does not, however, necessarily imply GEI with respect to the components of either the selection goal or the selection criterion.

Most national livestock evaluation programs focus on breeding value estimation for individual traits rather than for composite traits or indexes. Since multiple trait selection indexes may be based on either phenotypic values or individual-animal breeding value estimates for component traits, this approach facilitates design of customized indexes within different production systems. Such an approach is appropriate whenever GEI at the level of the component traits is less pervasive than that observed at the level of the selection objective. Clear interactions of environment with breed and with lines within breeds have been demonstrated in beef cattle and sheep (Panish et al., 1983, 1985; Hohenboken and Clarke, 1981; Hulet et al., 1974), but definitive interactions of sires within breeds with fixed environmental effects, such as region or breed of mate, have not been convincingly demonstrated within the context of national cattle or sheep evaluation.
If animal genetic effects interact with fixed, definable environmental effects such as region or breed of mate, the industry's response will depend upon the magnitude of the interaction and upon the population structure. In strongly regionalized populations where GEI is clearly recognized and where flow of breeding stock across environments is limited, use of environment-specific genetic evaluations is clearly indicated. In contrast, if the population is a national or international population with extensive movements of germplasm among environments and with apparently modest levels of GEI, the course of action is less clear. This situation appears to conform to that observed in U.S. beef cattle. In such a situation, subdivision of data to provide environment-specific evaluations would require subdivision of progeny and relative data on individual animals and would therefore reduce accuracies of evaluation. The magnitude of this reduction in accuracy would vary in proportion to the extent of movement of individual or gametes across environments. In particular, breeding value estimation for animals moving from one environment to another would be postponed until the animal produced progeny in the new environment. For general-purpose, national breeds such as those common in North American beef production, this situation is clearly undesirable and has in part been responsible for reluctance to come to grips with GEI in genetic evaluation programs. In North American beef breeds, the genetic correlation between sire performance across regions or breeds of mate has generally exceeded .60 (Tess et al., 1979; Massey and Benyshek, 1981; Bertrand et al., 1985, 1987). In industries which are not strongly regionalized and in which the genetic correlation among environments is substantial, environment-specific genetic evaluations do not appear indicated. A preferred approach is to recognize that performance for a single trait in multiple environments is analogous to performance for multiple traits in a single environment and to use multiple trait breeding value (BV) estimation procedures to accommodate GEI. If a reasonably small number of environments or production systems can be defined, and if pairwise genetic correlations among them can be estimated, all available data can be used to estimate performance in any one environment, and resultant accuracies of evaluation will properly reflect observed levels of GEI. Still, such an analysis should be conducted only in the presence of clear GEI, since BV estimation for multiple traits across multiple environments may tax computing facilities, forcing a choice between multiple trait analysis ignoring environmental distinctions or single-trait, multiple-region analyses. A different situation exists when environments of interest are random in nature, as in the case of sire x herd interactions. In this situation (Dickerson, 1962) one can only select for average performance over the array of environments, recognizing that selection response will not be optimal within any one herd or flock. In this setting, rate of genetic improvement in overall (i.e., across environment) performance is a function of the intraclass genetic correlation (rg) among environment and of the number of environments in which testing occurs. As rg declines, an increasing premium is placed on testing of individuals (either via relatives or progeny) in several environments. This situation is largely met within the North American beef industry where relatively widespread AI in seedstock herds generally ensures testing in a variety of environments. In sheep, the more limited use of AI and the generally greater regionalization of populations suggests that a conscious
Efforts to test sires in multiple environments may be important in national evaluation programs. For even very large stud flocks, the existence of significant flock x sire interactions would place a premium on recovery of animal performance data from a number of customer flocks. Use of half- or full-sib males in multiple flocks can provide an acceptable system of ties among flocks (Wood, 1986) but is still less efficient than use of direct sire ties achieved via AI.

Efforts to assess GEI have usually involved field data sets in which multiple sires have been used in multiple environments. This approach is acceptable, but requires widespread sire use in all environments prior to evaluation. A more efficient procedure may favor early experimental evaluation of GEI by using proven sires in environments different from those in which they were tested. Mahrt et al. (1990) and Notter and Cundiff (unpublished) have evaluated relationships between sire BV estimates derived in seedstock herds and observed progeny performance in crossbreeding under commercial conditions. Results suggest that BV estimates for growth and maternal traits from seedstock herds are excellent predictors of crossbred performance in matings involving Hereford and Angus cows in temperate North America. Similar studies involving Bos indicus or dairy breed dams, and performance in subtropical or other regions are needed to clarify appropriate responses to potential GEI. For example, Tilsch et al. (1989) reported that the genetic correlation between performance of progeny of beef bulls in purebreeding and in crossing with dairy breeds was considerably lower than expected.

In summary, GEI is to be expected at the level of net merit, but may be less common at the level of the component traits. BV estimation for component traits should therefore precede BV estimation for net merit. The nature of GEI will define the appropriate response in national breeding programs. For fixed environments, separate genetic evaluations may be necessary when populations are strongly subdivided, but use of multiple-trait procedures will be preferred when movement of animals among environments is common. If environments are random, selection must be for average genetic merit and testing across random environments is required. Testing of proven sires in novel environments can provide information on extent of GEI and on usefulness of existing BV estimates.

WITHIN- AND AMONG-BREED SELECTION

Selection of breeds for use in breeding programs has traditionally been based on breed mean characteristics, and has preceded choice of sires from within breeds and subsequent development of within-herd selection procedures. However, current national genetic evaluation programs in cattle and sheep have provided BV estimates for large numbers of animals of many breeds. Also, use of the BV estimates in selection has generated substantial genetic trends within breeds (Wilson and Willham, 1986; Nadarajah et al., 1987; Elzo et al., 1987), and the size of these trends appears to differ among breeds (Notter, 1989). Thus choice of individuals for use in breeding programs may now involve both average breed characteristics and the relative positions of candidate individuals within the respective breeds.

The choice of breeds for use in crossbreeding programs or composite lines has been discussed by Moav (1966a,b,c), Alenda and Martin (1981) and Kinghorn (1980). The case of simultaneous selection within and across breeds with consideration of differential realization of heterosis in specific matings has also been discussed by Kinghorn (1983, 1987).
In general, the multibreed selection index of Kinghorn (1983) and the across-breed EPDs (EPD = expected progeny difference = one half BV) later described by Notter (1989) have similar goals. Each is designed to evaluate overall additive merit of individual candidates for selection based upon the mean additive merit of candidate breeds plus the estimated BV of individuals relative to their respective breed means. Additionally, each recognizes that for use in commercial production, sire BV will depend upon the genotype (breed composition) of potential mates. Kinghorn (1987) further addresses the problem of optimum mate selection and of long-term genetic improvement within composite lines (Kinghorn, 1982, 1983). Both Kinghorn (1982) and Notter (1989) consider the potential for GEI, such that available BV estimates on candidates for selection may not be perfect predictors of crossbred performance.

If both within- and across-breed variation are to be efficiently utilized for overall industry genetic improvement, current and past breed evaluations must be interpreted in light of existing national genetic evaluation programs. In designing breed comparisons, animals (predominantly sires) that are used should be representative of the breed as a whole. This objective is best achieved by attention to random sampling from breeds being evaluated but in practice, documentation of the true nature of the sample has been rare. Widespread availability of BV estimates for proven sires, however, suggests that sires used in breed evaluation experiments should be chosen on the basis of existing BV estimates. Breed evaluations are time-consuming and costly. Use of existing BV estimates to adjust for genetic trends within breeds can allow more efficient use of existing breed comparison data and can extend the useful life of such data.

Notter and Cundiff (unpublished) utilized data from the U.S.D.A. Germ Plasm Evaluation (GPE) Program (Cundiff et al., 1986) to assess the impact of sire sampling and within-breed genetic trends on estimates of breed differences. As an example, Table 1 shows mean EPDs for weaning weight for bulls used in the GPE Program and for all sires of each breed born in 1970 (and therefore approximately contemporary to GPE sires) and in 1984 (taken as representative of current proven sires). Actual performance levels of crossbred GPE progeny are also shown, as are mean performance levels after adjustment of the data by linear regression to the mean of all 1970- or 1984-

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<td>Angus</td>
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Table 1 Weaning Weights (kg) of GPE Breeds Adjusted for Genetic Trend and Sire Samplinga

a Regression of actual weaning weight on weaning weight EPD = .81 ± .15 kg/kg.

b Tarentaise sires were not available in sufficient numbers in 1970.
born sires of each breed. Sire sampling (i.e., difference between GPE and 1970 mean EPDs) was reasonable in most breeds and adjustment for sampling did little to change relative performance levels (i.e., comparison of GPE and 1970-adjusted means). Genetic trends (i.e., difference between 1970 and 1984 mean EPDs) were large in Angus and Hereford, but smaller in other breeds. Thus breed variation in performance declined from 1970 to 1984, and breed constants derived in 1970 would not be appropriate for use in 1984.

Techniques for simultaneous within- and across-breed selection require accurate and current breed performance data, plus explicit consideration of anticipated heterotic effects. Improved analytical techniques for estimation of the necessary parameters are being developed (Robison et al., 1981; Elzo et al., 1985; Komender and Hoeschele, 1989). Application of these techniques to both experimental and industry data should be emphasized to facilitate objective and comprehensive evaluation of livestock genetic resources.

Extension of EPDs across breeds will place a premium on improving comprehensiveness of current EPDs. In North America, EPDs are usually only calculated for relatively highly heritable output traits involving immature growth and maternal ability. Only litter size, but not fertility or lamb survival are explicitly considered in sheep. Input traits related to health, and mature female size and nutrient requirements are not considered, yet are extremely important in breed selection, regardless of their feasibility of measurement and/or level of heritability within breeds. In general, economic traits which show significant across-breed variation must be included in across-breed evaluations, even if they are not a part of current within-breed genetic evaluations.

Interest in use of multibreed composite populations as a source of seedstock has blossomed in recent years but merchandising of such composites is complicated by difficulties in comparative evaluation of animals relative to existing purebreds. However, if composite populations are formed using proven, purebred sires; if appropriate estimates of breed mean performance are available; if subsequent within-herd genetic trends can be estimated; and if appropriate adjustments for heterosis and epistatic recombination effects are available (e.g., Koch et al., 1985), then members of composite populations can be evaluated relative to contemporary purebreds, at least in the early generations of composite development. Evaluations of individuals from advanced composite generations should be augmented by direct comparisons with competing purebreds. Such comparisons should be feasible if the composite has been successful, and unnecessary if it has not.

Several structural and analytical issues must be dealt with before industry-wide EPDs can be implemented. These include the source and timeliness of breed comparison data and the expression of the accuracy of across-breed comparisons. Most efforts to calculate breed and heterosis constants have involved experimental data, or, for growth traits, information associated with bull performance testing programs (DeRose and Wilton, 1988). Although models exist for estimation of breed and heterosis parameters from field data (Robison et al., 1981), the designs of commercial crossbreeding programs are not necessarily compatible with estimation of these parameters. More importantly, in the U.S., genetic evaluations of beef cattle are under the auspices of the breed associations, leaving crossbred producers (seedstock or commercial) without a national data processing organization. In the U.S. National Sheep Improvement Program, crossbred data can be processed but is often not submitted due to the lower value of detailed performance data in commercial flocks.
Sewell Wright's shifting balance theory of evolution (Wright, 1978) might be paraphrased as follows. If a natural population is divided into small, largely isolated subpopulations, genetic drift and weak selection could cause those populations to differentiate in their array of allele frequencies. As the environment changed and different genotypes become favored, the partially differentiated subpopulations would provide genetic and phenotypic variation upon which natural selection could act. The net effect would be evolution towards adaptation to the changing environment. Whether Wright's scenario is correct with respect to natural populations or not, it does not seem to be the population structure that characterizes pastoral livestock industries of temperate, developed countries. Rather the pyramid model is a closer approximation to reality. Relatively small elite populations (or group of breeders) export superior (at least different) genetic merit to multipliers who in turn export that enhanced merit to the much larger commercial segment of the population. Where large scale AI with frozen semen is feasible, the multiplier tier can be bypassed, and the genetic lag between elite and commercial populations is reduced.

Our final task is to discuss the influence of population structure, on the rate at which genetic change can be achieved and disseminated through a population. Elsewhere in these proceedings, Nicoll (1990) argues that genetic change for a bioeconomic breeding objective can most easily be maximized in large, vertically-integrated, commercially-driven production enterprises. We do not contest this conclusion, but most pastoral livestock production (both seedstock and commercial) does not occur under those circumstances. In North America at least, the typical purebred herd and flock are rather small, and has too short an average life span to contribute much to genetic improvement of the population. Commercial populations vary dramatically in size. Most purchase sires (or male gametes) but select female replacements from within the population. Such female selection will result in genetic change; but with usual selection intensities and temporal variability in breeding objectives and selection criteria, net change is likely to be minimal.

The swine and poultry industries have evolved towards fewer and larger production units, with genetic management co-opted by integrated, corporate entities. The ecological and economic role of grazing animals as foragers is likely to preclude or at least retard this trend in beef cattle and sheep. Ownership units of these ruminants are likely to remain rather small, on average. The task of the geneticist, and of those seedstock producers who assume the role of genetic resource managers, becomes one of using such a population structure as effectively as possible, or modifying it in a cost-effective, achievable manner. Several general strategies seem possible.

A much larger proportion of the commercial beef cow population could benefit, through AI, from genetic merit already available and characterized through national, breed-administered sire summaries. In many situations, estrus detection remains a constraining factor, or results of available synchronization methods are too variable and therefore not predictably cost-effective. We advocate efforts to further enhance the success and to reduce the cost of AI technology. As better information becomes available on more bulls, and as it becomes more possible for cattle producers to purchase semen to meet precise specifications and needs, AI use may expand. In sheep, successful intrauterine laparoscopic insemination, allowing use of frozen
Producers should investigate alternatives to all-or-nothing AI schemes. Within a herd, for example, the appropriate proportion of highest ranking cows for maternal traits might be synchronized and mated once by AI to produce replacement daughters, with clean-up matings and all other cows in the herd mated to terminal or "growth and efficiency" bulls. Such a scheme would effectively impose a pyramid structure within the herd and provide for preferential multiplication of superior genes.

Related schemes, but involving natural mating, have long been advocated for large sheep populations under single ownership (Scott, 1970). Ewes are divided into A, B and C flocks, according to phenotypic merit for the breeding objective, often wool quantity and quality. Ewes in the elite A group are mated to highly selected rams of the same breed to produce population replacements. Ewes from the B echelon are mated to rams of lower merit to produce further replacements; while C ewes are terminally crossed to meat breed rams, and are replaced as feasible by daughters of higher ranking ewes.

As large a proportion of a total livestock population as possible should contribute data for genetic evaluations. Small average herd size again is a problem; the bull in a single sire herd is not being progeny tested. The large number of herds using multiple-sire breeding pastures also cannot contribute to genetic evaluations. We advocate research and development to allow incorporation of data from crossbred progeny into existing genetic evaluations. Most commercial offspring of a male are often crossbreds, so it is appropriate to rank males partly upon the merit of their crossbred progeny. Proper accounting would have to be made for breed effects, direct and maternal heterosis and maternal breed effects on phenotype, but a substantial addition could be made to data bases for national sire evaluation. More individuals could be evaluated, with greater accuracy.

Group mating schemes have been advocated (James, 1977) to increase effective population size and, as a consequence, selection intensity. Elite populations are formed by screening the most outstanding male and female individuals for the agreed-upon breeding objective from cooperating populations. The superiority of these highly selected individuals, compared to the populations from which they came, has been called genetic lift. In open-nucleus herds, sires used in the elite herd typically are born within that herd, and female entering the elite herd in each year include outstanding individuals from member herds as well as females born within the elite herd. In a closed-nucleus scheme, after the initial screening all male and female replacements come from within the elite herd. Such schemes are designed both to accelerate genetic progress and to enhance dissemination of that improvement back to member herds. Males surplus to the needs of nucleus and cooperator herds can be sold on the open seedstock market.

These schemes have achieved commercial acceptance in New Zealand and Australia, but few have been initiated in North America, despite their theoretical benefits. Part of the reason probably is the tradition for independence among North America seedstock producers, who may think of other breeders more typically as competitors than cooperators. Also, agreement on a breeding objective is prerequisite to a group breeding scheme, and such agreement would in many instances be difficult to achieve.
Emerging reproductive technologies (multiple ovulation and embryo transfer, embryo or semen sexing and embryo splitting and cloning) make elite populations even more attractive (Land and Hill, 1975; Nicholas and Smith, 1983; Taylor et al., 1985; Smith, 1986, 1988, 1989; Gearheart et al., 1989), whether they are group mating schemes or under private, corporate or public ownership. In theory, rate of population genetic improvement for a given trait could markedly be enhanced using these technologies, due to reduced generation interval and(or) increased selection differential and(or) increased accuracy of selection. This may be accomplished at the cost of increased rate of inbreeding, but mating schemes can be manipulated to limit inbreeding within defined bounds (Wooliams et al., 1989). The potential impacts of such technologies on rates of genetic improvement have been estimated for a variety of scenarios; to project their effects in others is not necessarily simple but certainly is possible.

Data recording that would not be practical within existing industry population structures (feed intake for example) might be feasible in elite herds using advanced reproductive technologies. Enhanced rate of genetic progress, consideration of economic traits that are difficult to measure, and potential for wide dissemination of genetically improved gametes could pay for expanded and sophisticated performance evaluation in elite herds.

Finally we might ask, somewhat tongue in cheek, if Wright was right? Genetic theorists and practitioners can use advanced technologies of gamete and embryo manipulation to designed selection strategies and population structures which dramatically should enhance rate of response to selection. This is beneficial to all concerned, if the chosen breeding objective is valid, foolproof, spatially and temporally uniform and not subject to genetic x environment interaction. However, such universal breeding objectives may not exist. Although "profit" and "efficiency" are acceptable to all livestock breeders, the complex of traits associated with maximum profit or efficiency is unlikely to be spatially or temporally constant, and may be subject to important macro- and microgenetic x environment interaction.

In Professor Wright’s shifting balance theory, subpopulations which differ genetically largely because of drift provide a storehouse of variation to be drawn upon when a changing environment favors evolution to different genotypes. Perhaps a number of elite herds should be formed, analogous to several pyramids sharing a common commercial population base, with the tip of each pyramid representing genetic excellence for a somewhat different definition of net merit. Also, no matter how effective potential high technology mating and selection programs may be, there will be breeders who elect to follow their own objectives, methods and conscience. Their herds, along with the several pyramids envisioned above, will maintain some of the genetic variation of Wright’s subpopulations. In the past, we often have been thankful for such "living insurance" when the main stream of a livestock species has wandered seriously off course.

REFERENCES