A breeding programme depends foremost on the definition of the breeding objective. The reliability of estimated genetic merit will be associated with the judicious choice of selection criteria, the accuracy of the recorded information, the model used to describe the biological processes relating the breeding objective and selection criteria and the prediction methodology used. Effective genetic improvement will further depend on the presentation of the processed information and its rate of adoption by the industry.

INTRODUCTION

Performance recording involves "the systematic measuring and recording of performance or indicators of performance traits. These records become a data bank and, upon proper manipulation and analysis, are used in selection and management programs" (Brinks, 1984). In this paper we discuss the development of breed improvement programmes in beef cattle and sheep by focussing on the definition of the breeding objective, the choice of selection criteria and the processing of the recorded information.

BREEDING OBJECTIVES

Definition of the breeding objective should be the first and crucial step in a breeding programme. A breeding objective is a weighted combination of traits which we desire to improve. The list of traits in the objective and their weights should be decided on purely economic grounds. All economic traits that exhibit variation should be considered for the objective including measure(s) of reproductive success. All factors that contribute to costs and returns should be taken into account when deriving economic weights, including feed consumption (James, 1986).

Relative economic values (REVs) can be determined from the partial derivatives of the profit equation (Moav and Hill, 1966). Smith et al. (1986) showed that the dilemma of different economic weights for different sectors of production (unit of product, animal, producer, investor, consumer) can be resolved by discounting extra profit from genetic gain by the change in output that can be achieved by rescaling the production enterprise and by considering all costs as variable costs. The economic weights derived from the profit equation or efficiency ratio are equivalent on this basis. Discounted gene flow (McClintock and Cunningham, 1974) or diffusion coefficients (McArthur and Del Bosque Gonzalez, 1990) can be used to allow for the time lag of gene dissemination and character expression through the herd or flock.

Early work on defining breeding objectives for sheep was based on gross financial returns per ewe for unit changes in the traits identified as contributing to profit with occasionally some adjustment for known marketing costs (Clarke and Rae, 1977; Morris et al., 1982). Modern grazing management has led to better utilisation of pasture and highlighted the
opportunity cost of feed. Much recent work has considered including feed costs (Ponzoni, 1988; Rae, 1988).

Ponzoni (1988) considered the effect of ignoring expenses associated with the livestock enterprise. The loss of efficiency of index selection was small for sheep but substantial for beef cattle. More importantly ignoring costs gives rise to over-estimation of the economic worth of genetic gains.

Animalplan (Johnson et al., 1989), allows the breeder to set up one or more breeding objectives of relevance to the breeding programme. Traits that may be included in a breeding objective cover a broad range of 'official' traits with an established base of research information to enable prediction of breeding values (BV). A set of 'standard' objectives for each breed within species is supplied as a default.

Woolplan (Lewer et al., 1986) was designed to meet the performance recording needs of Australian ram breeders of Merino and other wool breeds, and has a formally defined breeding objective comprising five traits, but with flexibility to place restriction on reproductive rate or fibre diameter or for user-specified REVs.

The general philosophy for beef cattle recording schemes has been to provide BVs for various traits and leave the decision on how to use them up to the breeder. Ponzoni and Newman (1989) derived breeding objectives for pasture grazing beef cattle. The main points from their study were that calving day made the greatest contribution to economic gain, the maternal component of carcass weight was negligible, and that several traits, notably cow feed intake, changed in the 'wrong' direction. Ignoring feed costs shifted emphasis from reproduction to growth traits, with consequent increase in feed intake. Loss of efficiency (18%) from ignoring feed costs is large enough to justify careful consideration of feed costs in the development of breeding objectives for beef cattle.

The B-Object program (Brash et al., 1990) has been developed to calculate REVs for beef improvement in Australia and to combine these with BVs derived from Breedplan (Nicol et al. 1985).

In the USA goals in beef production have traditionally been towards maximum production in the expectation of greater efficiency. The systems analysis approach (Cartwright, 1982) has questioned the appropriateness of this goal in terms of optimising total herd profitability within given resource restraints.

While it is important that all costs and returns are identified in a production system, the uncertainty of future returns and the production environment make it impossible to establish breeding objectives with great precision. This is not necessarily a problem unless changes in REVs are large (Smith, 1983). It is important for a national recording scheme to have the flexibility for breeders to specify objectives for their own flocks and herds according to their role in the industry.

**SELECTION CRITERIA**

The breeding objective must be defined in terms of those traits that we would like to improve regardless of their ease of measurement and degree of inheritance. Selection criteria consist of those characters, genetically correlated with traits in the breeding objective or phenotypically correlated...
with other characters, which provide a cost-effective increase in accuracy of prediction allowing for measurement difficulty.

Traits in the objective and characters used as selection criteria generally correspond, particularly for major production traits. Indirect selection can be used to select on the basis of measurements of traits not included in the objective, for example, when a trait in the objective is costly and difficult to record, not expressed until later in life, sex limited or lowly heritable. This is theoretically sound but can fall below expectations in practice (James, 1982), likely due to inaccuracies in the knowledge of (co)variance components. Indirect 'marker' characters are being used to select for resistance (or tolerance) to disease, for example, selection against facial eczema in New Zealand (Towers et al., 1983). Inclusion of such characters in an overall index will depend on research of relevant genetic parameters, and for a marker character of no economic importance in its own right, the index will be sensitive to poor estimates of parameters (Sales and Hill, 1976).

Prediction of body composition on the live animal is an important consideration for meat producing animals. Ultrasound techniques have been used as an indicator of leanness in sheep (Bennett et al., 1983) and a quicker, cheaper mechanical device is being developed (Uljee, pers. comm.). Adjustment of a performance character to a constant liveweight basis may have deleterious effects on liveweight itself. For example, selection for testes size, proportional to body size, may in fact retard the rate of body growth (McNeilly and Land, 1986). Selection on fat depth adjusted for liveweight can be expected to reduce fat depth and fat percent but at a cost in terms of response in carcass weight.

In the absence of accurate estimates of parameters a biological index has sometimes been used. Simm et al. (1987) investigated the use of product traits such as lean growth rate as a selection criterion in meat animals. This does not require estimates of genetic parameters or economic values for component traits and therefore may be more stable and of longer-term use than economic indexes. However, if there is imbalance in the coefficients of variation of the components, the most variable trait will tend to dominate the product and unless that trait also has the highest economic value then selection based on an economic index is expected to be more efficient than selection on the product trait. Thus, since leanness in cattle and sheep is usually less variable than growth rate, selection on growth rate alone is nearly as efficient as selection on the composite trait and without the extra cost of measuring leanness.

Some attempts have been made to utilise knowledge of the biology of traits in the prediction. For example, Turner and Young (1969) described a component model for greasy fleece production. While intuitively appealing, selection experiments based on component traits have been unable to surpass traditional methods of fleece weight selection (Davis and McGuirk, 1987). Furthermore, a selection experiment for leanness based on knowledge of the biochemical enzyme pathways involved in fat synthesis has demonstrated selection response equal to, but not greater than traditional approaches (Muller, 1986). This is likely a result of the increased requirements for specification of the model (particularly (co)variances) when a number of component traits are included.

Reproduction rate is a complex trait which has a large effect on the biological and economic efficiency of beef production and should be considered
in the context of an overall breeding objective where breeds are fulfilling a general purpose role. In the USA (Koch et al., 1986) and in Breedplan in Australia and Beefplan in New Zealand, most of the selection emphasis has gone on size and growth rate with some attention to calving ease and milk. An Angus Breeding Scheme in New Zealand has a breeding objective containing fertility and growth and selection criteria comprising individual weaning and yearling weights, dam's lifetime number of calves born and the maternal half sib average for weaning weight (Nicoll et al., 1979).

As shown by Ponzoni and Newman (1989) the deletion of female fertility from the selection index reversed the direction of change in fertility and the maternal component of carcass weight and halved the accuracy of the index. Reproductive rate has an important bearing on the total breeding operation - a low calving rate reduces selection opportunity. Testes size was suggested by Land (1973) as an indirect indicator of reproductive rate in the female. Purvis (1987) and Hammond and Graser (1987) have evaluated selection criteria for reproduction in sheep and beef cattle respectively. In Breedplan consideration is being given to provide BVs for scrotal circumference and days to calving as well as the opportunity to record serving capacity (Hammond, 1989).

Controlled release devices have been shown to give a reliable measure of group mean pasture intake. Current Australian work on sheep should yield information on the relationship between intake and body size and other production traits, so that food intake can be more accurately incorporated into the calculation of REVs (Lee et al., 1988). Inclusion of pasture intake in non-linear breeding objectives (output per unit of feed consumed) or linear objectives including a BV for feed intake, will likely require more accurate means of individual assessment than is available from estimates of faecal output (Parker et al., 1990).

DATA COLLECTION

Basic to the operation and efficiency of performance recording schemes is the accuracy of the data collection process (Uljee and Rennie, 1990). Unique animal identification is fundamental, both within and between flocks/herds to enable across flock/herd evaluation of animals. Pre-numbered check lists and edit checking are an integral part of data validation. Recent developments in data collection such as electronic weigh scales, data loggers and micro-computers have greatly facilitated data collection and validation on-farm and, if required, the downloading of that information to a central processing unit. Electronic identification systems have the potential for more rapid and reliable animal identification.

Pedigree recording is vital when combining performance of relatives although this is not always possible in extensive farming systems. To achieve accurate mating data, identification of the dam is critical. Chances of errors increase with multiple births and higher stocking rates, so for sheep it is necessary to establish dam-offspring links as early as possible. Real-time imaging technology can be used for pregnancy diagnosis and to determine the number of foetuses (Fowler and Wilkins, 1984).

The standardisation of collection of data from off-farm sources and its merging with on-farm data is an important consideration. The integration of performance recording with wool testing such as with Woolplan has been a prerequisite for acceptance of the scheme by Merino breeders.
There is a need for data entry to parallel farm practice so as to avoid selective recording. For example, two-thirds of the weaning weight records used in the 1988 American Simmental sire summary were from heifer calves.

In the short term, the main costs of measuring and recording will be associated with collecting and entering data and not with processing. Future developments in automated data capture to reduce keyboard usage for data entry and to provide error checking at source will enhance the accuracy of selection decisions.

**PREDICTION OF BREEDING VALUES**

The prediction of breeding values involves the conversion of pedigree and performance observations from a data bank into a measure which corresponds with the breeding objective. Breeding objectives are typically multiple trait, requiring prediction of each component of the objective to combine with REVs as appropriate.

Prior to numerical calculation of BVs, a model must be specified to summarise the biological processes that lead to observations on traits in the breeding objective and characters used as selection criteria. This model may include:

(i) **Model equation.** Commonly an additive equation including fixed (non-genetic) effects, genetic effects (BVs or functions thereof) and a residual effect.

(ii) **Variance-covariance matrices.** These describe the (co)variation due to genetic and residual effects for each measured character and genetic effects for each trait in the objective.

(iii) **Distributional properties pertaining to the random factors in the model.** It is often assumed that random effects follow a multivariate normal distribution. For example, Restricted Maximum Likelihood (REML) estimation of parameters in (ii).

Henderson (1973) described a sequence of methods which can be used for prediction in certain circumstances. These methods assume that the desirable properties of a predictor are a form of unbiasedness (expected value of estimated BV is the expected value of actual BV), and minimisation of the prediction error variance (PEV).

(i) **Best Prediction (BP)** minimises PEV, but requires unrealistic knowledge of the joint distribution of breeding values and observations.

(ii) **Best Linear Prediction (BLP)** is a restriction from BP to provide best prediction in the class of linear predictors. In the widely assumed case of multivariate normality, the BLP is in fact, identical to BP. The method is also commonly called Selection Index. Operationally, the values of the fixed effects (parameters) and the (co)variance components must be known.

(iii) **Best Linear Unbiased Prediction (BLUP).** Relative to BLP, the major difference with BLUP is that the values of the fixed effects need not be known. In practice, a further major difference from (earlier) implementations of BLP is that information from all relatives can be included in an animal's evaluation due to Henderson (1976) discovering a rapid method for inverting the numerator relationship matrix.

Bayesian techniques can be used to derive predictors for genetic evaluation (Gianola and Fernando, 1986). In practice, the computations may be rather formidable (e.g. Carriquiry and Harville, 1988), or else the predictors which have been derived are very like, if not identical to,
existing techniques. These techniques may not demonstrate any practical advantage over the fairly robust mixed model approaches when the model specification is, at best, a good approximation.

In practice, one never knows the model equation exactly. Furthermore, neither the fixed effects, (co)variance components or distributional properties of random effects are known with any certainty. For at least two decades, selection index computations have been applied to obtain BVs (e.g. Sheepplan, Beefplan) although the estimated BVs are not BLP because assumed values for fixed effects (from least squares), used to adjust data, and (co)variance components were not known without error. Increasingly over the last decade, a BLUP approach has been used for estimating BVs in sheep and beef cattle. This follows recognition that BLUP can be obtained by solving a set of Mixed Model Equations (MME), which can be formed without need for direct inversion of large matrices (Henderson, 1963). Furthermore, these equations are amenable to indirect (iterative) solution. In practice, the solutions are not BLUP as the (co)variance components are not known and the assumed model is only an approximation. Nevertheless, selection experiments and simulation studies would suggest that properties of the predicted BVs seem desirable. Further work is needed to validate commonly assumed models and investigate alternatives. For example, a negative environmental covariance between the weaning weight of a cow and her calf has been documented (Magnus and Brinks, 1971; Johnsson and Obst, 1984) but is not included in any genetic evaluations to our knowledge.

In some instances, the observed variable is not continuous and assuming normality seems unreasonable, e.g. number of lambs born in sheep and calving difficulty score in cattle. Two approaches have been used. One is to assume normality regardless, perhaps after accumulating categorical measures over lifetime performance as Sheepplan/Animalplan does for number of lambs born. The other approach is to assume an underlying normal distribution with thresholds which map the continuous variable on the observed categories. This threshold model is desirable from a philosophical viewpoint but experience suggests the resultant breeding values do not markedly increase selection efficiency (de Boer, 1988).

There is considerable evidence from field data of a relationship between sample mean and variance. This suggests that linear models based on raw data cannot assume fixed (co)variance components. One approach is to transform data to a scale which may be more appropriate, (e.g. logarithm). This has other implications such as assuming the model equation is multiplicative, and thus changes the distribution of random effects. Another alternative, used in the national evaluation of American Simmental cattle, is to transform the incidence matrices (Quaas et al., 1989). This enables adjustment for weight traits which can be measured in both sexes but demonstrate mean and variance differences by sex. In general, it needs to be confirmed that genes responsible for performance in the sexes are highly genetically correlated. Genotype-environment interactions may also exist between management techniques and regions. These warrant considerably more attention from researchers.

The industry structure (two-tiered, three-tiered, open-nucleus, group breeding scheme, sire reference) specifies requirements of BVs for within- or across-flock/herd use. In the sheep industry, BVs have historically been used on a within flock-year basis. In these circumstances, BLUP probably has little more to offer than BLP, provided BLP implementations use information from all available relatives. Increased interest in sire-reference systems and artificial insemination (AI) has resulted in greater need for BVs which
are comparable across flock-years. In the North American beef industry, greater acceptance of AI created the need for across-herd and time evaluations. In Australasian production systems utilising beef cattle, natural mating remains well established with some interest in AI for a small percentage of cows to allow across-herd comparison and introduction of outside sires.

Increased expertise and computational requirements for national evaluations have led in many cases to a stratified approach to prediction of BVs. Interim BVs, suitable for within-herd use are calculated in the first stage, with rapid turnaround to breeders. These within-herd BVs may require as input, previous evaluations and reliabilities from across-herd evaluation (Henderson 1975a). At less frequent intervals, a national evaluation provides across-herd evaluation. This has occurred in beef cattle and to some extent in sheep. This two-stage prediction has increased the rate at which micro-computer packages have been developed and used for within-herd evaluations (Robinson and Chesnais, 1988). Micro-computer evaluation has been made possible by development of algorithms which require less memory than the traditional approach of forming MME (Schaeffer and Kennedy, 1986), a procedure now being adopted for national evaluation of dairy cattle. Furthermore, two-stage evaluations ensure retention of a central database which is prerequisite for further research such as in variance component estimation.

The use of frozen semen creates a need for BVs which are comparable across-time to a greater extent than was the case with natural mating whereby candidates for selection were mostly contemporary. This can create additional problems in evaluation of animals because expected BVs change with time as a result of genetic trend. This is not a problem when complete pedigree information is available but is a problem with open-nucleus breeding schemes whereby animals are continually screened in from unrecorded commercial sources. A solution is the addition of genetic groups (Westell et al., 1988) to the model equation such that animals with unknown parents are not necessarily treated as contemporary. Such groups should probably be applied in sire-reference and group breeding analysis of sheep.

Extensive breeding programmes often practise multiple joining of sires to a group of females. Henderson (1988) outlined an approach for modifying the relationship matrix based on assumed joining ratios. This technique is adopted in Breedplan. In the case of embryo transfer, the model for evaluation of traits for which maternal effects are important must distinguish between natural and surrogate dams (Schaeffer and Kennedy, 1989). When genetically identical animals are included in a population, the genetic evaluation under an animal model is complicated by the fact that the relationship matrix among animals is singular. An equivalent model based on genotypes rather than animals can be used (Kennedy and Schaeffer, 1989).

The MME technique will provide BVs unbiased by preferential mating provided data used for preferential mating decisions are made available for the complete analysis. In some cases when records are available for a number of years there is some question as to how far back one should go. It is likely that the use of all historical records adds little to the efficiency of the analysis relative to using records sufficiently far back to account for preferential mating of the parents of the current generation.

The accuracy of prediction can be increased by including (correlated) multiple trait observations in the prediction of each individual trait in the
objective. However, this will typically increase the size of the problem to be solved by a factor of the number of traits included. In selection programmes whereby selection criteria become available at different ages, there is opportunity for breeders to practise sequential culling. This multi-stage selection results in inferior animals being culled at one or more times, thereby only a selected fraction are actually available for measurement of a later trait. Henderson (1975b) has demonstrated that BLUP can, under special hard to define conditions, account for selection of this kind provided, as a minimum, that all the characters on which selection was based are included as selection criteria. Simulation studies (Pollak et al., 1984) have demonstrated that these results seem to stand up in practice.

In some domestic animals it is known that major genes are segregating and the population of interest may include both homozygotes and heterozygotes (e.g. Booroola F-gene in sheep). Prediction based on indices which include a prediction of the genotype for the major gene have proved little different from selection indices which ignore the possible presence of a major gene (Shi et al., 1990). It would appear there may be little payback in terms of response to selection from trying to identify any major genes contributing to important components of the breeding objective.

In many populations there are desirable genotypes which can be formed from crossing animals of different breeds. In some cases these crosses have ultimately developed into synthetic breeds in their own right. However, in other cases, for example to exploit heterosis or stratification in an industry, there may be repeated crossings. These crossbred performance records may be excluded from analysis of purebred merit, or treated as a contemporary group in their own right, thereby removing the average effect of heterosis. An alternative would be to evaluate for specific combining ability. Kinghorn (1982) developed a multibreed selection index by incorporating crossbreeding effects into selection index framework. Further research is required to verify that BVs estimated in a crossbred population are highly correlated with BVs for the same animals in the straightbred population. A genetic correlation close to unity has been calculated for some weight traits in Simmental and Simmental-cross calves (Garrick et al. 1989).

**REPORTING OF BREEDING VALUES**

Breeding values must be reported in such a way as to assist breeders in better fulfilling their objectives. This requires that the BV be easily interpreted relative to the breeding objective. There would seem little justification for functions of BVs when these functions are in a sense an arbitrary objective such as the maternal grandsire merit of 0.5 BV(direct) + 0.25 BV(maternal).

Ideally, a total merit index should be presented if REVs are known, and perhaps a superiority ranking. The question of base may arise - whether an average BV should be zero or 100 and whether the base is held constant or floated, intentionally or inadvertently (Quaas and Pollak, 1988). This makes little difference from an academic viewpoint but may be important if breeders are used to comparing rankings obtained from analyses in different years.

A graphical approach to presenting merit has been applied in the New Zealand Dairy Industry. Two stylised normal distributions (triangles) are used to display the distribution of progeny BVs from the use of an average
bull relative to the use of a particular bull. A graphical representation for ram evaluation is used by the Texel breed association in France.

Accuracy of BVs may be presented in terms of a reliability, PEV or effective progeny number. The effective progeny number is likely to be the most easily understood measure, and is useful for demonstrating sequential culling when multiple trait selection criteria are involved. In practice, the accuracy is of little use to the breeder unless risk is being accounted for. In this case, it is the prediction error covariances that are likely to be more critical. Computationally these are difficult to obtain during indirect solution of MME, and in any case are difficult to report. However, they could be usefully incorporated into computer programs to choose a team of sires while incorporating risk, such as the portfolio theory used in some dairy industries (Schneebberger et al., 1982).

Breeding values can also be summarised in such a way as to demonstrate genetic trend (average BV by year of birth) and perhaps genetic merit by flock/herit. This provides breeders with a useful guide to genetic improvement. An alternative, simpler approach, would be to calculate actual selection differentials achieved for each trait and overall index, relative to theoretical selection differentials based on the animals' records actually observed in their flocks/herds (Dodd and Delahunty, 1983). This enables a measure of efficiency of selection in summarising the extent to which selection is practised on information not made available for genetic evaluation such as conformation and teeth/feet. A slightly more sophisticated approach is to calculate an index in retrospect (Dickerson et al., 1954) to demonstrate exactly which traits have received attention, and indicate possible breeding objectives actually being used.

CONCLUSION

The success of a breeding programme will ultimately depend on the ability of the breeding manager to use the processed information to identify those individuals which are expected to produce offspring best suited to the breeding objective. Further developments in methodology and computing technology should improve the effectiveness and speed with which data are processed.

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