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EVALUATION OF INTER-FLOCK GENETIC IMPROVEMENT PROGRAMS FOR SHEEP AND GOATS

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SUMMARY

Some of the factors involved in inter-flock or breed improvement programs are discussed. Such programs are complicated by the fact that sheep and goats produce a wide range of products under diverse environmental, management and economic circumstances. This leads to problems in defining realistic breeding objectives arising from determining the beneficiaries of genetic improvement, the major genetic decision makers in the industry and the relative importance of the various productive characteristics. The implementation of functional performance recording systems, breeding systems to generate young sire replacements, and testing systems to disseminate genetic improvement, also depend on the conditions under which the breeding programs operate. Alternative means of estimating genetic improvement in breeding programs through comparisons of progeny by sires repeated over time or from parents of different ages, and the use of artificial insemination (AI), multiple ovulation and embryo transfer (MOET) and mixed model methodology (BLUP) are also briefly addressed.

INTRODUCTION

The farming of sheep and goats is characteristically distributed in the more difficult agricultural environments, either in temperate regions (over 60% of the world sheep population) or in arid, tropical and subtropical regions of the world (80% of the world goat population) (Devendra and Coop, 1982). In these areas, sheep or goat farming is often the only form of animal production, although extensive beef cattle production systems may complement or compete with sheep or goat production. The environmental, economic and technical conditions under which sheep and goats produce implies that these species are usually less intensively farmed relative to the increasing intensity of production in beef cattle, dairy cattle, pigs and poultry. It is therefore not surprising to find that the overall efficiency and intensity of sheep and goat breeding schemes relative to those of the other species follow the same trend.

The genetic improvement of sheep and goats is therefore often complicated by the fact that the typically extensive farming systems, coupled with the production of a wide range of products, are strongly environmentally dependent. This leads to problems: firstly in defining breeding objectives, for breeds must not only be productive, but must also be adapted to the environment; secondly in recording data under extensive conditions, and finally in implementing a breeding program which assumes that a breeding structure exists in the population.

In addition to a priori optimization of selection objectives, methods and dissemination, the evaluation of a breeding program implies that the economic elements of risk, perspective and return on investment have also been considered. A review of sheep or goat breeding programs cannot be attempted in strict
economic terms because, unlike cattle programs, there is little published work in this area (Barlow, 1982). It has been suggested that most breeding programs represent sound investment opportunities when quite small improvements are disseminated to a large population (King, 1985). An alternative means of evaluation relies on the traditional technical aspects of breeding programs.

Most information available on industry genetic improvement programs is based on sheep; hence discussion will concentrate on this species.

'ROLE OF THE BREEDING PROGRAM IN THE POPULATION

Change in the genetic merit of a population is closely linked with the structural characteristics of the population. The ideal demographic structure of a population under selection has been studied by several authors using different models according to whether the selection system was stabilized (Smith, 1960; Bichard, 1971; Jackson and Turner, 1972; Elsen, 1980) or was in an establishing phase and hence subject to fluctuations in selection response (Hill, 1974; Elsen and Mocquot, 1974). Simulation models can be used to identify the optimal movement of animals, according to their probable genetic contributions to future generations within the hierarchical structure of the industry. In sheep and goat populations, animal movement in the hierarchy has invariably been established before the implementation of a structured breeding program has commenced. Historically, breed societies have played a major role in this regard, which results in new genetic improvement plans being viewed with reservation or being adopted only slowly (Barton, 1984). When genealogical data are available, demographic studies can identify the relative contributions of foundation animals to the present population (James, 1972) and hence the role and status of various flocks in the industry. Only a few such studies have been made in sheep or goat populations (Vu Tien Khang and Barillet, 1979; Dureau, 1984).

The structure of the breeding population can also be described by a simple ratio relating selection intensity to the extent of performance recording influencing the accuracy of selection. Ratios such as candidate rams to total rams ($I_1$) measuring the recording effort, or selected rams to candidate rams ($I_2$) measuring the selection pressure, or the product of these ratios ($I_3 = I_1 \times I_2$), indicating the extent of selection in the population, have been used to characterize the selection conducted in some sheep breeds in France (Flamant and Elsen, 1979) and in New Zealand (Carter and Cox, 1982). These ratios are easily obtained, and when compared with values defining potential genetic progress or national benefit, can give a first assessment of any breeding program.

In the long term breeding plans may seek to establish a compromise between the utilization of genetic variability through selection and the maintenance of genetic variability for future gains. Short-term control over the loss of genetic variability through inbreeding in a selected population may be accomplished through the avoidance of some close matings, but at a cost to the potential rate of gain. Such mating systems effectively make the inbreeding coefficient more uniform among individuals of a given generation, and only delay the rate of inbreeding in the population as a whole (Robertson, 1961). Although an accurate description of the permitted matings used in a breeding plan is important, only retrospective genealogical studies on the actual data will indicate the efficacy of such efforts. These analyses are usually restricted to experimental populations where permitted matings are assumed to have been
better controlled and/or where inbreeding trends may be precisely analyzed (Lamberson and Thomas, 1984). Nevertheless some studies have included commercial populations (Vu Tien Khang and Barillet, 1979; Lamberson et al., 1982).

The formal development of genetic improvement programs has received attention in the literature only relatively recently (Cunningham, 1982). In defining the breeding objectives of a program, the population structure within which the long-term consequences of genetic improvement develop, and the beneficiaries of this improvement, have not often been defined (Danell, 1980).

In industries of developed countries, and those of developing nations where local sheep or goat populations have differentiated into cohesive units in the initial process of breed evolution (Lerner and Donald, 1966), the structure of the breeding system is generally hierarchical in nature. Selection decisions are made in the nucleus tier at the apex of the hierarchy and the products of this selection (predominantly males) are distributed to a larger commercially-oriented tier. In some cases an intermediate level may exist between these two tiers which multiplies the nucleus stocks to provide males (and occasionally females) to the commercial tier.

The distinction between levels in the breed hierarchies of many established industries has often been based on breed society registration of pedigrees. In these situations, the dissemination of genetic improvement is restricted to a downwards direction from the nucleus tier. However, many registered pedigree flocks in the upper levels of the hierarchy are small in size, affecting selection intensity, and are limited in the extent to which performance records are used, influencing selection accuracy (MLC, 1972; Carter and Cox, 1982; Delport et al., 1984). In addition, there may exist a reluctance to change from more traditional breeding methods and goals, particularly by successful breeders established in the nucleus level of the breed hierarchy. These features can be counterproductive to applying planned industry genetic improvement programs. It is noted however that the registration barriers between tiers can be replaced by those based on performance. That this can be achieved on an industry basis without losses in momentum of industry participation, even when flock sizes are small, is illustrated by the Norwegian and Icelandic sheep industries (Gjedrem, 1969; Jonmundsson, 1986).

BREEDING OBJECTIVES

Many conflicts are involved in establishing breeding objectives for sheep and goats. The definition of breeding objectives is influenced by the beneficiaries of genetic improvement and the identification of the major decision makers in the improvement program. Objectives have often been quantified from the commercial producer's point of view, since decisions are made at the farm level (Ponzoni, 1982). However, in industry or national breeding programs, central financing for breeding and production may be decided at the national level with objectives consequently set for collective or national benefit, such as lower consumer prices, product quality specifications or total efficiency of production (Danell, 1980). Formulation of a national breeding objective requires a longer term perspective than can be tolerated at the farm level. However, the objective must still have relevance to the decisions made at the farm level if a national program is to remain viable in the long term. Generally, however, the risk of a nil return at the national level is low (Smith, 1978).
Conflicts of interest can arise between the various tiers of the hierarchi­
cal population structure since genetic decisions are generally made by breeders
in the nucleus rather than at the level of the commercial user, the consumer or
even the nation. For instance, nucleus breeders may indulge in selection
practices aimed at promoting 'standards of excellence' or phenotypic
'marketability' that are of no ultimate economic value to the commercial flocks
(Barton, 1984). Further conflicts can occur between breed hierarchies in
crossbreeding situations. Ponzoni (1982) illustrated this conflict with the
Suffolk breed in Australia, where nucleus Suffolk flock breeders are interested
in female reproductive rate, but the commercial users of the rams are not
because all crossbred progeny are slaughtered. Similarly, in the Tarasconaise
breed in France, nucleus flocks select for adaptability to a mountainous envir­
onment, but overall productivity is desired when surplus ewes are transferred
to better environmental conditions for crossing with terminal sire breeds.

Even within tiers the decision on breeding objectives is not always
unanimous. Net returns can vary widely at the farm level according to environ­
mental conditions and management and breeding systems, such that breeders may
tend to define their own individual set of breeding objectives. A further
difficulty is that apart from special purpose breeds and breeding systems, sheep
and goat farming is mainly a dual-purpose fibre/meat or milk/meat enterprise and
the relative importance of each trait will depend on the environmental condi­
tions and the breeding system applied, as well as on the relative returns of the
different traits. The close dependence in sheep and goats between production
and environmental conditions also means that adaptability to the environment
is of importance when considering breeding objectives, whereas in other livestock
species a more artificial environment tends to be adapted to the animal.
Genetic variation in adaptability traits may be worthy of investigation in an
attempt to reduce labour and management costs, particularly in extensive farming
systems.

Once breeding objectives have been defined, subsequent selection applied in
a breeding program should be evaluated carefully since traits in addition to
those in the objective may be unintentionally selected for. For example, Elsen
et al. (1986a) reported that although prolificacy was the most important trait
considered in the breeding program of the Lacaune sheep in France, young rams
born as twins were unintentionally being culled. The calculation of selection
indexes in retrospect (Dickerson et al., 1954) is informative in this regard,
particularly if data exist on traits additional to those included in the
selection criteria. Such studies have been reported for sheep populations
(Elkje and Clarke, 1986; Elsen et al., 1986b).

The results of retrospective analyses give indications of where selection
emphasis has been placed by breeders in the program (particularly in relation
to the defined objective and desired selection criteria), and the relative
efficiency with which selection decisions are being made at the flock level.
It should be noted however that these analyses cannot distinguish between the
relative reductions in selection pressure resulting from losses of selected
animals, reproductive failure or selection for non-recorded traits considered
to be important by breeders (e.g. structural features). Furthermore, the
analyses may assume that selection occurs in one step whereas selection is a
succession of events from conception to culling which apply to each of the four
basic pathways of the selection process (Rendel and Robertson, 1950). All must
be considered particularly on an inter-flock basis. Despite the suggestion
that improvement programs should include female evaluation (Steine, 1982a), most
national breeding programs only consider male selection pathways, leaving the
breeding flocks themselves to make selection decisions on the female side. According to Steine (1982a), female selection in Norway contributed considerably to overall genetic gain (15% for growth rate).

RECORDING SYSTEMS

The diversity of environmental conditions, production systems and products that exist in sheep populations has resulted in a variety of performance recording systems in different countries (Owen, 1971; Croston et al., 1980). The authors are only aware of four national on-farm goat performance recording systems in Norway (dairy goats; citation by Shelton, 1978), France (dairy goats; Ricordeau et al., 1979), South Africa (Boer goats; Campbell, 1984) and more recently in New Zealand (Angora and Cashmere goats; Callow, 1985). Under extensive farming conditions in difficult environments, practical problems in animal identification may limit the application of comprehensive recording systems.

Industry performance recording schemes for sheep may be broadly classified according to the type of selection and level of recording possible: individual selection or selection using information from relatives. In the former case, recording systems rely on breeding value estimates of individual characteristics (liveweight, fleece weight, litter size, etc) without identification of ancestors or progeny, or without the use of such information. This type of recording system was most common in the selection of yearling sheep for meat and wool traits in the survey of European schemes by Croston et al. (1980). Other on-farm recording systems may use records on both the individual and its ancestors and/or progeny. Some of the more comprehensive systems of this type are the national flock recording schemes in Norway and Iceland (prolificacy, carcass traits and fleece weight), New Zealand (prolificacy, growth rate and fleece weight) and France (prolificacy, growth rate and milking ability). The New Zealand and French recording systems also have various options to include data from off-farm sources such as fiber-testing laboratories in New Zealand (Clarke, 1985a) and individual performance testing stations in France (ITOVIC, 1983). The same features of New Zealand's national flock recording scheme (Sheepplan), together with the supplementary fiber testing option, have also been adapted for Angora and Cashmere goat breeders (Goatplan; Callow, 1985).

Despite the importance of sheep and goat meat production in many countries, recording systems for specialized meat breeds have lagged behind those for other meat species (Kempster, 1981). Growth rate is the characteristic most commonly recorded on-farm, with little attention being given to carcass characteristics (Rae, 1984a). The same is true for the Boer goat in South Africa (Campbell, 1984). Consumer demand for lean meat has imposed a requirement to consider reduced carcass fatness in recording systems, but few schemes appear to have yet responded to this challenge. The Norwegian sheep recording service annually progeny tests 2300 ram lambs on the basis of an index which includes lamb carcass weight, eye muscle area, weight of hind quarter and kidney fat weight (Eikje, 1977; Steine, 1982b). The fatness measurement is included as a restricted trait in the index. New Zealand's Sheepplan offers an option for lean meat production using an index of lean tissue growth which incorporates liveweight and subcutaneous fat depth measurements (Rae, 1984b; Purchas et al., 1985; Dodd et al., 1985). The same methodology is also being applied in Australia (Harris, 1985).

Milk production from sheep is mainly concentrated in the Mediterranean area,
although information on recording systems is limited. Flamant (1984) described a selection scheme within the French Lacaune breed which relies predominantly on recording milk yield, but is now also including data on milk composition in response to an industry requirement to value milk on the basis of cheese yield (Barillet, 1985).

Recording systems provide information to aid selection decisions, but Steine (1982a) considered that they should also function as flock management information sources if user interest and participation is to be maintained over time. Rapid data turn-around times and frequent attendance of farm recording or extension officers enable recording systems to fulfill this role, particularly in France (Cournut and Martin, 1983; Bodin et al., 1986) and in Spain (Perez Almero and Valls Ortiz, 1977).

In addition to the cooperation of users, the success of any recording system will depend on the extent to which records are used in selection decisions. Two New Zealand studies examined the efficiency of ram and ewe selections; in six flocks during the establishment years of the National Flock Recording Scheme, the forerunner to the present day Sheeplan (Eikje and Clarke, 1986) and more recently in the Sheeplan-recorded nucleus flocks of eight cooperative breeding schemes (Dodd and Delahunty, 1983). In both studies, efficiency was defined as the ratio between the actual and maximum possible selection differentials. Eikje and Clarke (1986) reported low selection efficiencies for weaning weight and fleece weight in rams (36%) and ewes (38%) during the early years of the national flock recording scheme. For the selection index at 2-years of age (which incorporated ewe reproductive rate as well as weaning weight and fleece weight), Dodd and Delahunty (1983) reported ranges in selection efficiency of 64-74% in rams and 27-44% in ewes among group breeding schemes using Sheeplan, a later version of the national recording scheme in New Zealand. The increased efficiencies over time probably in part reflect an increased breeder confidence in use of records as an aid to selection.

BREEDING SCHEMES

In effect, breeding programs represent the application of genetic specialization based on the principle of assortative matings between elite males and females to produce the next generation of replacements, particularly young sire replacements. The aim is the effective application of the four selection pathways to the dissemination of genetic merit. However, the implementation of this principle often depends on the conditions under which the program is operated (e.g., the structure of the breeding population and average flock size).

Within-flock Structures

In its simplest form, a breeding system may consist of ranking females within flocks on the basis of their performance and the mating of elite females and males in order to select young replacement males. The efficiency of this system depends on the selection intensity realized on the female side, but an additional feature is the potentially short generation interval on the male side. At the breed level, such a system can evolve into a cooperative venture where young males resulting from elite matings within flocks are subsequently distributed to other flocks via centralized rearing centers. This concept has been successfully applied in France (Flamant and Elsen, 1979) and in Spain (Perez Almero and Valls Ortiz, 1977). Screening the same proportion of elite females within flocks avoids flock environmental effects but does not take advantage of genetic differences among flocks (which may become reduced if sires are shared.
efficiently over time). This system gives all flocks the opportunity to contribute to breed improvement with consequent advantages in maintaining breeder interest and cooperation. Such a breeding system is particularly useful when production or environmental circumstances prevent sire-progeny links to be made for the ranking of sires. However, as flock size increases, difficulties may arise in managing elite ewes on each farm such that breeders may prefer to centralize their elite females in a nucleus flock.

**Nucleus Flocks**

The open nucleus or cooperative group breeding scheme concept has been widely promoted in the New Zealand and Australian sheep industries (e.g. Rae, 1976) and more recently for fiber-producing goats (e.g. Clarke, 1985b; Nicoll and Wickham, 1985). The principle is to identify ('screen') elite females on productive merit from a large base population and to locate them in a central nucleus flock from which males are bred and supplied back to the contributing flocks. The genetic properties of open nucleus breeding systems have been reviewed by James (1982) and Mueller and James (1984a).

Screening from a large contributing population conserves additive genetic variation for the scheme as a whole enabling more rapid expected genetic gains compared with closed structures such as traditional systems based on breed society registration. Open nucleus systems typically have a greater selection differential on the females to breed males path which more than compensates for a reduced differential on the males to breed females path (James, 1977). Operating structures for open nucleus breeding systems that optimized selection response have been reported for various situations (e.g. Jackson and Turner, 1972; Rae, 1974; James, 1977). These studies showed that the general conditions of about 10% of the population in the nucleus, half of the nucleus female replacement transferred from the base, and surplus nucleus-born females transferred to the base, were close to the optimum. In terms of ultimate selection response, considerable flexibility existed around these optima.

While 'opening' a nucleus contributes to improvement per se, additional contributions can be made when the nucleus also uses more efficient selection strategies and shorter generation intervals (Hopkins, 1978). Furthermore, the rate of inbreeding is less in an open than in a closed nucleus system. James (1977) showed that in an open nucleus with optimum structure the effective population size is about twice that in a closed nucleus system of the same actual size.

Two studies in Australia and New Zealand have shown that investment in an open nucleus sheep breeding system is likely to be profitable (Jones and Napier, 1980; McArthur, 1983). For example in the New Zealand study, McArthur (1983) compared the continuation of an existing open nucleus sheep breeding system (base population of 209 000 ewes), with reversion to purchasing rams from the breeding industry. An equivalent annual return of $3.75 per ewe ($800 000 annually) was expected for the open nucleus system, with only a 2.5% chance that the system would not be economically viable.

Like collaborative breeding ventures in France and Spain, group breeding schemes in New Zealand and Australia have experienced additional non-genetic advantages (e.g. Parker and Rae, 1982). Such groups enjoy an identity greater than that of an individual breeder, enabling more effective purchasing of supplies, utilization of specialist technical and advisory services, and the potential to capitalize on and exercise influence in research, commercial and political areas.
Open nucleus breeding systems appear to be well suited to large flocks farmed under extensive conditions. Thus in contrast to the previous breeding system where elite females are maintained and intensively recorded within flocks, open nucleus systems can function satisfactorily with little on-farm recording commitment in the contributing flocks. This assumes that the basic recording conducted in the contributing flocks accurately identifies the elite females for screening into the nucleus. In sheep breeding programs placing emphasis on reproductive performance for example, the identification of ewes producing multiple births can be accomplished with little recording effort. Detailed performance recording and selection can then be maintained in the one environment in the nucleus flock.

Testing Systems

For traits with a low heritability, limited to one sex, or which cannot be accurately predicted on the live animal, genetic improvement can be enhanced through the progeny testing of males. This leads to increased costs of management and recording, and usually to an increased generation interval for males. Progeny testing is technically and economically justified if the accuracy of estimated sire breeding values is enhanced more than enough to offset the increased generation interval and if sires used in different flocks can be compared on a between-flock rather than a within-flock basis. Avoiding this sire-flock confounding effect is a major feature of breeding programs applying progeny tests.

The benefits of progeny testing for breeders of sires for meat production from crossbred lambs was reported by Rae (1976). Relative to individual selection on weaning weight, an increased genetic gain of 40% was expected when 25 ram lambs were tested annually in an outside flock over 500 commercial ewes. Such a system provides an opportunity for several small ram breeders to collaborate in a common progeny testing program. Rae (1984a) cited an additional study comparing progeny testing for number of lambs born in New Zealand dual-purpose breeds, with the rate of improvement achieved by selection on the average of the dam's records. In a 10,000 ewe scheme, progeny testing 18-month rams increased the annual genetic gain by 8-10%, testing ram lambs increased the gain to 20-22%, while the use of AI (1 ram to 1000 ewes) to provide more widespread dissemination of proven rams further increased the gain by 28%.

Mueller and James (1984b) formally examined progeny testing in an open nucleus system when selecting for a single trait measurable in both sexes. These authors cautioned that progeny testing should be evaluated solely as a means to increase selection accuracy. In cases where AI is used (increasing the selection differential) and is assumed to be a necessary consequence of progeny testing, comparisons of progeny testing with individual selection may underestimate the relative gains from individual selection itself.

In order that technically sound comparisons of sires can be made across flocks, breeding programs must operate within the limits imposed by their industry; e.g. average flock size, environmental and production conditions, degree of breeder cooperation, etc.

In industries characterized by small, intensively-recorded flocks, progeny testing must be conducted across flocks, as applied in the ram circle concept in Norway (Gjedrem, 1969). Rams are circulated among cooperating flocks in order to spread the progeny of each ram over many flocks. In 1980 there were 117 ram circles in Norway, annually progeny testing 2300 ram lambs on some 12 to 13% of the sheep population (Steine, 1982b). However, in industries with large
flock sizes such as in New Zealand and Australia, sires could be progeny tested within flocks, provided that single-sire mating groups can be accommodated in the management system. Foulley and Bibe (1979) and Foulley et al. (1983) have shown that if more than six sires representing the same population are tested per flock, the necessary links between flocks to estimate sire breeding values across flocks reduces in importance provided that the relationship between the sire and the flock in which he is used is assumed to be random. In general, New Zealand and Australian sire-breeding flocks do not satisfy this condition since there is considerable use of home-bred sires and little planned use of sires between flocks. However, interest in the use of AI in these countries is increasing with the advent of sire referencing methodology and large-scale insemination techniques (Clarke et al., 1984). Under these circumstances, sire referencing through AI, in conjunction with the use of homebred sires, will enable across-flock breeding values to be estimated for both the AI and homebred sires.

LeVier (1984) described the implementation of a large-scaled sire reference system for Merino sheep in Western Australia. The system aids the industry in providing information on between-flock genetic differences to identify potential sources of high-merit sires, both for efficient selection of replacement reference sires and for participants contemplating a change in the source of purchased sires. Additional advantages include a potentially greater selection intensity of reference sires since replacement rams can be selected from all participating flocks, and the possibility to examine the importance of genotype x environment interactions. AI is an important component of the system, which relies also on advances in the insemination of frozen semen directly into the uterus (Maxwell, 1985).

Sheep breeding programs that have exploited the genetic advantages of AI for some time are characterized by a close integration between breeders and the industry they serve, such as the programs for the Lacanau dairy sheep in France and the Icelandic sheep breed in Iceland.

An interesting variation of the principle of across-flock comparisons is the maintenance of a genetically stable flock for Merino sheep in South Africa (Erasmus, 1976). Rams from this flock are used in breeders' flocks to enable progeny comparisons with homebred rams to be made. This system is perhaps more a tool to estimate flock effects and genetic progress in different closed flocks (Poggenpoel and Van der Merwe, 1984), than a breeding program per se.

Central performance testing may endeavour to overcome the problems of across-flock selection by evaluating animals under a common environment. Such facilities have more often been exploited to select males on the basis of growth and wool traits, such as in the United States (Shelton, 1984a). In Australia, central tests for wool production (wether competitions) have created interest in productivity components, although they have been of less value in estimating between-flock genetic differences (Jones et al., 1980). Central testing is also practised for meat production in Boer goats in South Africa (Campbell, 1984) and for fleece productivity in Angora goats in the United States (Shelton 1984b), as well as for growth rate of young ram lambs in France (ITOVIC, 1983). In a review of sheep recording in European countries, Croston et al. (1980) concluded that the advantage of accurately measuring genetic differences between individuals in central performance testing was outweighed by the limitations of the capital expense in establishing and maintaining a station, and of the small proportion of the total population which can be tested at one time. Further limitations of central tests relate to the possible carry-over effects of the pre-test environment on test performance (Dalton and Morris, 1978), and the
limited predictive value of a ram's test performance. Preliminary data from Illinois have indicated that there was little relationship between ram average daily gain on central test and progeny gain to 120 days of age or progeny carcass merit (Thomas et al., 1984).

EVALUATION OF GENETIC PROGRESS

Controlled experimental selection studies with sheep have shown that genetic progress can be achieved for such traits as reproductive rate (Clarke, 1972), wool traits (Turner, 1977) and liveweight (Pattie, 1965). However, under the field conditions in which national breeding programs must operate, the estimation of genetic gain is more difficult and few studies have reported such estimates.

One method is to compare the divergence of performance over several years between flocks in the breeding and commercial sectors. An essential assumption is that environmental changes over time are similar in both sectors. Nicoll (1983) reported such simple estimates for reproductive rate in a large commercial open-nucleus sheep breeding system in New Zealand, expressing estimates as within-year deviations from commercial hill country flock statistics. Regression coefficients on year were 0.027 and 0.018 lambs weaned per ewe present at lambing for the nucleus and base flocks respectively.

An alternative method is to compare the progeny of selected and commercial sires out of common dams in a common environment (e.g. Clarke, 1978; Hight, 1982). The difference in performance enables the genetic lag between breeding and commercial flocks to be estimated, which is related to genetic change. An additional use of this method, which is of considerable extension value is to demonstrate to commercial producers the expected advantages from using sires selected from within the breeding program, thus assisting in the dissemination of genetic merit into the population.

Other methods reviewed by Tixier and Ollivier (1984) are available for data recorded in breeders' flocks. Such methods may be classified as either using progeny records of a sire mated over several years compared with contemporaries assumed to be progressing by selection (Smith, 1962), or comparing performances of contemporary progeny from parents of different ages. Both methods assume linearity of genetic change, and among other things, no selection of sires and dams on progeny performance. In an industry situation however, the repeated use of sires generally involves high merit sires joined with the better dams, although this bias may be reduced by taking into account sire and dam ages, and the dam's generation number. The accuracy of the estimates of genetic trend will also depend on the extent to which repeated sires are used. Where repeat mating intervals are short and the turnover rate of sires is high, the degree of generation overlapping per sire is low with a consequent reduction in the accuracy of the estimate of genetic gain.

Estimates of industry genetic trends based on comparisons of contemporary progeny from parents of different ages have been reported by Eikje (1975) and Eikje and Steine (1976) in Norway. The estimation procedure included an adjustment to account for the possible effects of unequal selection of parents. The annual trend estimates for the more important traits were 0.25 kg (weaning weight), 0.24 kg (carcass weight at 160d), -0.01 kg (kidney fat weight), -0.02 kg (fleece weight), 0.007 lambs born and 0.023 lambs weaned per ewe lambing. The small negative trend in kidney fat weight was expected since it is included as a restricted trait in the ram indexes of the breeding program, but the negative
An alternative means of estimating genetic progress in a national breeding program when generations overlap is to use individuals originating from previous generations of selection through AI or embryo transfer. Frozen semen has generally not been widely applied in sheep and goat breeding programs to date because of poor conception rates. However, the success of laparoscopic intra-uterine insemination with frozen semen has recently contributed to an expansion in the use of AI in Merino sheep in Australia. Maxwell (1985) reported that some 50,000 ewes were inseminated with frozen semen by laparoscopy under commercial conditions during the 1984/85 breeding season. In such situations, the genetic life of elite sires may be extended to enable sufficient overlapping of generations to estimate genetic trend by the methods previously discussed. In other situations, frozen semen inseminations from reference sires, which constitute a constant genetic base over time, may be conducted at regular intervals. The precision of the estimated genetic trend will depend on the time period that elapses between the test inseminations (i.e. the interval between the ages of parents producing the contemporary progeny; Atkins et al., 1986). In order that progress in the breeding program is not compromised to estimate genetic change, such matings could be organized in commercial flocks where, combined with current generation elite and commercial matings, they would enable the estimation of both genetic progress in the program as well as the genetic difference between nucleus and commercial tiers in the hierarchy of the population.

The use of multiple ovulation and embryo transfer (MOET) in sheep and goat breeding programs has received relatively little attention compared with beef cattle (Land and Hill, 1975) and dairy cattle (Nicholas and Smith, 1983). However, interest in the technique as a means of multiplying scarce sheep and goat genetic resources is gaining momentum in New Zealand (e.g. Tervit et al., 1986a,b).

Considerations of the benefits of MOET in sheep and goat improvement programs may require less conventional approaches to the selection of replacements as described for dairy cattle by Nicholas and Smith (1983). Increased litter sizes would provide the opportunity for early selection of replacements based on comparisons with contemporary sibs. Any reduction in selection accuracy may be more than offset by a shortened generation interval (Nicholas, 1985). From an industry point of view a national open nucleus flock, derived through MOET from assortatively mated elite parents in the industry, could be used to multiply and disseminate young sires to the industry, provided the industry accepted greater genetic variability in the young sires produced and did not demand only well-proven sires. Alternatively, the nucleus could be used as a national source of young sires in situations where an organised progeny testing program is established. As noted by Land (1982), the efficiency of disseminating genetic improvement throughout a population will determine the extent to which MOET will improve the rate of selection response.

Formal comparisons of MOET regimes with existing breeding programs based on say, individual selection or progeny testing, may need to account for possible changes in the structure of the breeding system. Applying the argument of Mueller and James (1984a) with respect to comparisons of progeny testing, any beneficial responses (e.g. due to changes in population structure or generation interval) that are introduced together with MOET, should not be attributed to it directly (ElSen et al. 1984). This review suggested that few spectacular genetic improvements of breeding plans would result from MOET in sheep.
Nevertheless the technique has the potential to assist in the estimation of genetic trends, particularly in avoiding the present disadvantage of measuring changes in breeding values of sires when mated to dams of different generations. When associated with embryo splitting or cloning and storage, MOET may enable the same genotype to be compared in different environments (which may in fact be different selection generations) on a large and meaningful scale.

The success of mixed model methodology in separating genetic and environmental effects to predict breeding values free of environmental influences is in part dependent on genotypes being represented directly or indirectly (through relatives) in different environments. Accurate relationships between animals need to be included in the mixed model equations (the numerator relationship matrix). Thus, known relationships among individuals recorded in different environments can be exploited to generate rankings of predicted breeding values across environments.

Using BLUP to predict breeding values within flocks enables rankings to be made across years, and hence estimates of genetic trend are possible. In this case the numerator relationship matrix incorporates all relationships among animals, including contributions to relationships from both sires and dams (the animal model). Blair and Pollak (1984) noted that the computations involved in the full animal model can be reduced if the equations for animals without progeny were absorbed (a reduced animal model, RAM). These equations may be further reduced to a set of single-sex prediction equations with consequent advantages in computational efficiency (R. Thompson, pers. comm.).

In the context of national breeding programs, BLUP methodology can also be used to predict across-flock breeding values and genetic trend estimates, provided that genetic ties exist among flocks. Such links predominantly occur on the male side particularly in industries using AI, although open nucleus breeding systems may also establish links on the female side through the transfer of ewes to and from the nucleus. Thus, the random effect of breeding value of the animal in the animal model changes to the random effect of sire (the sire model), and the sire contributions in the numerator relationship matrix increase in importance. Although the sire model is simplified in principle relative to the animal model, the extent and expense of the computations involved may be prohibitive for some sheep breeding programs. The accuracy of the genetic trend estimates will depend, among other things, on the strength of the genetic links across flocks (i.e. the distributions of progeny across flocks).

BLUP methodology has been applied and used to estimate genetic trend in dairy cattle (Henderson, 1973), beef cattle (Kennedy and Henderson, 1977) and pig populations (Ludenhaim and Eriksson, 1984), but applications to commercial sheep breeding programs are yet to be published. Rae and Anderson (1982) advanced three major reasons for the lack of adoption of BLUP in sheep breeding programs: (i) multi-trait breeding objectives are common in sheep which complicates the prediction of breeding values, particularly where continuous traits are combined with sex-limited categorical traits such as number of lambs born; (ii) the adoption of BLUP estimation of breeding values increases computational overheads, and appear to be greater still when estimating genetic trend (Atkins et al., 1986); and (iii) without the widespread use of elite sires through AI, the incentives and potential for using BLUP in national sheep breeding programs are not as great as would otherwise be the case.
CONCLUSIONS

The goal of breeding programs is to allow dissemination of improvement down a hierarchy from relatively few breeders to many commercial producers, whose products are distributed to the consumer population. Evaluation of industry breeding programs is complicated by the fact that breeders, producers and consumers view the merit of programs from different positions and by such diverse criteria as physical performance, sociological aspects and economic criteria (Hill, 1981). In sheep and goat populations, the close dependence of production and management systems on the environmental conditions experienced by these species has disadvantaged them relative to the establishment of comprehensive breeding programs for other livestock species such as dairy cattle, pigs and poultry.

Few sheep and goat breeding programs have been subjected to economic appraisal. The work of Elsen and Mocquot (1974) and Barlow (1982) deserves attention, since as a basis of evaluation, economic assessment of inter-flock genetic improvement programs encompasses most aspects of quantitative genetics, and further aspects from several other disciplines in animal production and economics. There is need for further work in this field.

Immediate and universal adoption of current technology described in this review may not be as directly applicable in less developed countries. Environmental, productive, economic and social conditions may warrant a different approach to the problem of national genetic improvement but one that may be just as radical under each particular set of circumstances. It has been shown here that the more developed countries for which information is available have achieved a level of specialization in their industries using a variety of techniques and organizational structures. Different features may need to be considered in many cases to match the full environmental background of adaptative and sociological circumstances of the stock and the people. It may be desirable, for example, to initiate a program based on dissemination of genetic merit to village flocks through AI via local research institutions and rearing centers. Inseminating technicians could then provide important extension contacts to encourage sound genetic selection and husbandry decisions. The same basic operational and technical considerations apply to all breeding programs, the commitment and cooperation of breeders and servicing personnel being the essential ingredient for successful industry-wide implementation.

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