THE UTILISATION OF BREED RESOURCES IN THE IMPROVEMENT OF SHEEP PRODUCTIVITY

Utilizacion de los Recursos Raciales en la Mejora de la Productividad Ovina

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NEW ZEALAND

As more results comparing different breeds are published, more crossbreds studied and new breeds developed, the literature on sheep breeds and strains has become enormous and beyond the bounds of any meaningful detailed review. The situation is somewhat in contrast to other farm livestock, especially pigs where fewer breeds are now involved due to increasing standardisation, intensification and specialisation of the pig industry (Sellier, 1976). This contrast is hardly surprising in that sheep provide fibre, meat, milk, skins and dung for fertilisers or fuel over a wide diversity of production systems throughout the world. These range from nomadic and transhumance systems of Europe and tethered systems for utilisation of crop wastes in Asia and Oceania, to highly intensive grassland farming and production from stall-fed and housed animals (Rae, 1952; Sierra, 1974; Taneja, 1974; Treacher, 1974; Devendra, 1979; Turner, 1980).

BREED UTILISATION

As Rae's (1952) review emphasised, much sheep production takes place through the exploitation of semi-natural or often unfavourable hill and mountain environments in which a large number of breeds has evolved to become adapted to local conditions of climate and food supply. Crossing has taken place in attempts to improve indigenous stocks through grading-up of coarse-woolled native breeds to the Merino, favoured because of its pre-eminence as a wool producer, and the development of new improved mutton breeds from slow-maturing native stock using especially the Leicester and Southdown breeds. Introduction of exotic breeds to improve fecundity has been a particularly active field of study during the past 10-15 years.

The importance of adaptability to severe conditions has placed emphasis on within-breed improvement but crossbreeding has also been used as methods of husbandry and economic circumstances change. Thus, the breed composition of New Zealand's sheep industry, for example, has altered markedly during its short history in response to grassland development and changing market demand for meat versus wool (Clarke and Meyer, 1982). These changes in breed distribution can be remarkably rapid (Carter and Cox, 1982) which is one of the major strengths of breed utilisation through crossbreeding. Ch'ang and Atkins (1982) stress this aspect for sheep production in Australia where crossbreeding occupies a pivotal role to allow the simple and quick transfer of breed resources from the wool to the meat producing sectors of their sheep industry.

INDUSTRY STRUCTURES

Probably the most advanced systematic application of crossbreeding for sheep production occurs in the sheep industries of Australia and the United Kingdom where aged ewes from hill flocks are mated to specialised breeds such as the Border Leicester to produce F1 ewes which are in turn mated under better conditions to special-purpose terminal sires for production of three-way cross lambs for slaughter (Bichard, 1974; Fogarty, 1978). Accordingly, the Suffolk and Border Leicester breeds have developed from original localised types to breeds...

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having a major role as special-purpose male lines in an industry-wide cross-breeding programme.

While the U.K. has a long-standing tradition of crossbreeding it is only recently that the component advantages have been carefully evaluated and understood. Close analysis has revealed considerable regional variations and some surprising departures from the generalised industry structure (MLC, 1972). This study showed that 43% of ewes were mated to Down rams, nearly 80% of these being Suffolks which also sired 27% of crossbred ewes compared with the 33% sired by Border Leicesters. Hill breeds comprised 38% of all ewes and contributed directly only 18% of carcass meat, but indirectly through crossbreeding their total genetic contribution to lamb meat supply was 36%; to the dams of slaughter lambs it was 57%.

Analyses in other countries where even simpler levels of industry stratification may apply (Sierra, 1974; Timon, 1974; Carter and Cox, 1982; Terrill, 1982; Hanrahan, 1982) have also revealed areas of priority for future advancement through breed change, crossbreeding strategy or selection.

BREED COMPARISONS

The U.K.'s MLC study also revealed that past breed performance data were severely limited, many being on-farm trials in which breed and management differences were associated. There was little data on the importance of genotype x environment interaction implied by the large number of local breeds and crosses maintained. Wiener and Hayter (1975) also highlighted a lack of comprehensive crossbreeding studies, especially for hill breeds, in the U.K. Similar situations exist in other countries as indicated by the reviews of experimental evidence presented at the 1980 World Congress on Sheep and Beef Cattle Breeding (Ch'ang and Atkins, 1982; Clarke and Meyer, 1982; Hanrahan, 1982; Hofmeyr, 1982; Terrill, 1982).

Maijala's (1974) review of papers presented at the 1974 Working Symposium on Breed Evaluation and Crossing Experiments showed, for 31 breeds, very wide variation in performance. Regardless of the production system, breed differences in prolificacy were almost invariably of considerable economic significance with important breed variation in fleshiness and fat cover of meat also being evident. Much of this variation arose from the extremes set by the very fecund dam breeds although the experiments of Wiener and Woolliams (1982) showed that breed variation was significant even for breeds which had been developed for similar ecological niches. To this list should be added breed differences in milk production (Flamant, 1974), ability to breed out-of-season (Ch'ang and Atkins, 1982), wool production and fleece characteristics (Woolliams and Wiener, 1981).

Rae and Land (1980) also note the considerable effort that has been devoted to experimental evaluation of breeds and crosses during the past 10-15 years. Improved development and understanding of the theoretical bases of breed evaluation and utilisation (Bichard, 1974; Carter, 1976) have in turn encouraged experimental research, as have advances in disease control and semen storage permitting readier international exchange of genetic material. All have emphasised the facility and precision with which breed differences may be utilised (Dickerson, 1973). Their exploitation is also likely to be very cost effective in comparison with other methods of improvement, breed differences often being equivalent to many generations of effective selection.
RECENT NEW ZEALAND EXPERIMENTS

In New Zealand on-farm testing and experience were the basis of early breed developments which were largely based on the philosophy that an intermediate between the existing and new parental breeds would be better adapted to prevailing husbandry and market circumstances. Thus, the Corriedale, Perendale, Coopworth, South Suffolk and South Dorset Down breeds were developed although prior to the 1960's there was little comparative information on the relative productive merits of breeds and crosses. Experiments on an adequate scale to provide meaningful estimates of genetic parameters relevant to breed utilisation strategies are even more recent (Clarke and Meyer, 1982).

Dual-purpose Breeds

Two large experiments at the Woodlands and Templeton Research Stations produced contemporary purebred and reciprocal F1 ewes which were evaluated in matings to Down breed rams (Clarke et al., 1982). Breed means by sire of the ewe whose performance was being analysed, averaged across all ewe breeds contributing to the breed or first-cross gave the results presented in Table 1. They indicate different breed rankings for meat production, wool production, body size and overall productivity.

| [Table 1] |
| Purebred and crossbred performance (reciprocals averaged) in the Woodlands trial is summarised graphically in Figure 1, the position of the alphabetic symbol indicating their average values. This further highlights, for example, the superiority of Romneys and Romney crossbreds for wool production and of Border Leicester and Cheviot crossbreds for lamb production and illustrates the considerable opportunity for different combinations of meat and wool producing genes offered by these breeds. |

Since wool and meat production are both important to sheep farming costs and returns, especially in N.Z., it becomes important to reach an overall assessment of productive merit (Clarke and Meyer, 1982). The negative sloping line shown in Figure 1 represents a constant overall productivity (iso-contour) assuming a ratio of wool to lamb prices of four. Thus, genotypes which are equidistant at right angles to and on the same side of this line are of equal productivity; those which are further above it are more productive than those which are closer. On this basis, Romney-Border Leicester crossbreds were about 10% more productive overall than Romney-Cheviot crosses.

Results from the Templeton trial (Table 1 and Figure 2) provided further important evidence of genetic variation among breeds and crosses. For example, Dorsets displayed similar overall productivity to Romneys and Corriedales, their superior weaning rate and lamb growth rate being compensated by inferior wool production.

Not all aspects of relative performance are embraced by these results. For example, the high milk production and leanness advantages of Dorset (Geenty and Jagusch, 1974; Geenty et al., 1979) are not fully reflected in the weaning weights presented in Table 1. These will be better expressed under production circumstances favouring artificial milking and more tangible market rewards to the producer, respectively. Nevertheless, it is clear that taking joint account of both meat and wool production and of body size has considerably altered breed differences in overall merit and that first-crosses have retained a useful advantage over purebreds.
Figure 1
Meat and wool production of purebred and first-cross ewes at Woodlands (see Table 1 for symbols)

Figure 2
Meat and wool production of purebred and first-cross ewes at Templeton (see Table 1 for symbols)
Relative 120day lamb liveweight
(Sd = 100)

Relative lamb fleece weight
(Sd = 100)
Table 1 - SIRE BREED MEANS ACROSS PURE AND FIRST CROSS (2-4 YEAR OLD) EWES
(from Clarke et al. 1982)

<table>
<thead>
<tr>
<th>Mating wt (kg)</th>
<th>No. Lambs weaned</th>
<th>Wt Lamb weaned (kg)</th>
<th>Fleece wt (kg)</th>
<th>Productivity</th>
<th>Productivity/Ewe wt</th>
</tr>
</thead>
<tbody>
<tr>
<td>Woodlands Experiment Romney (R) 52.1(100) 1.11(100) 24.2(100) 3.87(100) 39.7(100) (100)</td>
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<tr>
<td>Border L. (B) 55.7(107) 1.20(108) 26.8(111) 3.68 (95) 41.6(105) (98)</td>
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<tr>
<td>Cheviot (Ch) 51.9(100) 1.17(105) 25.0(103) 3.16 (82) 37.6 (95) (95)</td>
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<tr>
<td>Merino (M) 46.0 (88) 0.99 (89) 21.0 (87) 3.70 (96) 35.8 (90) (102)</td>
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<tr>
<td>Templeton Experiment Romney (R) 58.6(100) 1.06(100) 26.5(100) 3.69(100) 41.2(100) (100)</td>
<td></td>
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<tr>
<td>Corriedale (Co) 60.4(103) 1.05(100) 26.4(100) 3.70(100) 41.2(100) (97)</td>
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<tr>
<td>Dorset (D) 62.8(107) 1.12(106) 29.2(110) 2.89 (78) 40.8 (99) (92)</td>
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</table>

Productivity = Wt Weaned + (4 x Fleece Wt)

Figure 3 - Sire Breed Rankings for Romney and Romney-cross Lambs at Ruakura (Carter and Kirton 1975, Carter and Cox 1982). (Sire breed codes: BL = Border Leicester, Ch = Cheviot, PD = Poll (and horn) Dorset, DD = Dorset Down, EL = English Leicester, Ha = Hampshire, Ln = Lincoln, Me = Merino, Ro = Romney, Ry = Ryeland, Sd = Southdown, Sf = Suffolk, SD = South Dorset Down, SS = South Suffolk)
Meat Breeds

An extensive series of N.Z. trials was conducted to compare growth rate and carcass merit of crossbred lambs at 3½-6 months of age (Carter and Kirton, 1975). In line with overseas trials, breed differences in lamb progeny liveweights broadly reflected those of the sires themselves although Dorset, Cheviot and Southdown crosses showed more rapid early growth while English Leicester and Border Leicester crosses and purebred Romneys showed less rapid lamb growth than expected from adult ram body weights.

Breed differences in conformation, carcass grading and carcass composition were, under the conditions of these trials, of lesser economic significance than slaughter weight, by far the most important determinant of carcass return. However, important differences occurred between breeds in progeny survival which influenced carcass weight per ewe (Figure 3(a)). For example, compared to their performance for 120-day liveweight, lamb survival improved the ranking of Southdown relative to Hampshire crosses in terms of carcass weight per ewe lambing. [Figure 3]

Also, when judged on total lamb wool plus carcass productivity, indicated by the iso-contour through the Southdown x Romney mean (Figure 3(b)), Border Leicester crosses demonstrated an economic superiority similar to some of the larger Down breeds. Thus, even for meat breeds, wool production returns can influence overall breed rankings.

PROLIFICACY RELATIVE TO EWE MATING WEIGHT

Other N.Z. results (Clarke and Meyer, 1982) have shown a wide range in ewe prolificacy for the same breeds in different environments and a close association between prolificacy and mating liveweight. Because there appears to be a strong between-year and between-stocking rate basis to this association, breed differences in prolificacy will be much reduced when breeds are farmed at comparable mating weights. The importance of variation in prolificacy to genetic variation in lamb production (Hanrahan, 1982) underlies the practical significance of this association. In addition, deliberate husbandry variation in mating weight is of considerable importance to the efficiency of meat production from sheep, there being some evidence for differential breed responses in ovulation rate (Hanrahan, 1982; Smith et al., 1982). Such circumstances severely complicate the conduct of critical breed evaluation trials.

Despite these generalisations some of the genotypes reviewed by Clarke and Meyer (1982) had a high prolificacy relative to their mating weight suggesting possible advantages in terms of their efficiency of meat production. These were animals derived from the high-fecundity Finnish Landrace and Booroola Merino breeds and strains whose prolificacy had been improved by successful within-breed selection (Clarke, 1972).

HIGH FECUNDITY BREEDS

The fecund Finnish Landrace and Romanov breeds have been seen in many countries as a rapid way of combining growth, conformation, wool and adaptability attributes of local stock with genes for improved prolificacy (Jakubec, 1976). Improved out-of-season activity and shorter interval between lambing and next fertile oestrus are additional advantages under accelerated lambing (Land, 1978). Early trials in the U.K. indicated that "reproductive performance of Finn crossbreeds was much higher than in contemporary traditional crossbreds, but they showed higher lamb mortality, lower milking ability and slower lamb growth rate" (Smith et al., 1979). These drawbacks and their different appearance lead to their poor acceptance in practice.
Like many fecund breeds, the Finn has inferior wool production (Meyer et al., 1977) which, although partially compensated by some wool quality attributes (Hofmeyr, 1982), can influence its optimum contribution as a crossbred. Environmental circumstances can also be important to this balance through, for example, their influence on lamb survival (Nitter, 1975). In the U.S.A., ewe costs per kilogram of market lamb were reduced by 20-25% compared with Rambouillet half-breds, improved lamb survival generally making-up for deficiencies in lamb weaning weight (Dickerson, 1977; Terrill, 1982). Under poor range conditions and with severe climatic exposure at lambing, F1 Finnsheep crosses have raised nearly as many lambs as F1 Finnsheep and had a longer productive life. The precocity of yearling halfbred Finn ewes has been particularly outstanding under poorer nutritional conditions.

The Booroola Merino is another interesting breed which arose from a flock of Australian Merinos selected for high fecundity (Turner, 1978, 1982). It has been much studied recently in Australia and N.Z. (Piper et al., 1979; Piper and Bindon, 1982a; Allison et al., 1982) and is receiving increasing attention from N.Z. producers (Clarke, 1982c). Physiological research (Bindon and Piper 1982a, 1982b) indicates somewhat different characteristics in comparison with other high fecundity genotypes, recent genetic evidence pointing to a single major gene affecting ovulation rate (Piper and Bindon, 1982b; Davis et al., 1982).

Rendel (1980) has recently summarised the results of a Food and Agricultural Organisation Survey on Prolific Sheep Breeds under the leadership of I.L. Mason. It points to the common intensive features of their management - small flocks under close observation. Most seem to have early sexual maturity, absence of lactational oestrus, high male libido and good conception rates in addition to their high prolificacy. This wide range in alternative genotypes augurs well for improvement of fecundity in various locally adapted sheep breeds.

PREDICTING CROSSBRED PERFORMANCE

Crossbreeding is utilised in practise to take advantage of heterosis and/or breed differences in additive genetic merit. Their separation is often difficult (Terrill, 1982), but usually important if alternative methods of utilising breed differences and their interactions are to be anticipated (Dickerson, 1969). Bichard (1974) has summarised the considerable recent theoretical developments in the design, analysis and understanding of crossbreeding systems. Experimental designs for the estimation of genetic parameters have been discussed by Dickerson (1974), Hill (1974), Carter (1976), Nitter (1978) and Cundiff (1982). In addition, Nitter and Fewson (1974) and Sellier (1976) stress the confounding which exists in many designs and the relative experimental precision of some alternative approaches.

The separation of performance into characteristics of the individual's own genotype and those of its mother has been important to the genetic understanding of crossbreeding (Rae, 1974), although confusion of terminology sometimes arises between the concepts of individual heterosis in a maternal trait and heterosis in a maternal effect on individual performance, especially when this performance attribute is itself a reproductive or similar maternal characteristic.

First-cross Performance

Estimates of heterosis for sheep meat production were extensively reviewed by Nitter (1978), later results from some comprehensive on-going trials being summarised by Ch'ang and Atkins (1982) and Wiener and Woilliams (1982). Nitter's (1978) summary indicated an average superiority of 18% for weight of lamb reared per ewe exposed in reciprocal crossbred compared with purebred matings,
the heterotic advantage being similar for the average performance of F1 cross-bred ewes relative to the parental purebreds. Most of these advantages arose from improved survival of crossbred lambs and fertility of crossbred ewes, respectively, although small increments in other components of meat production tend to be cumulative rather than compensatory (Wiener and Woolliams, 1982).

Thus, Ch'ang and Atkins (1982) found, relative to purebred matings, that lamb production (kg lamb weaned per ewe joined) was increased 2% in crossbred matings, 37% in matings by first-cross rams, 60% in matings to first-cross ewes and by 81% in matings among first-cross rams and ewes. Advantages to crossbred over purebred sires were also reported in the reviews of Nitter (1978) and Terrill (1982), arising from improved lamb survival, effective working life and with some unconvincing evidence for better prolificacy and fertility as well.

In the N.Z. trials at Woodlands, average superiority of first-crosses over purebreds for lamb production, wool production, productivity and ewe body weight was 28%, 7%, 20% and 8% respectively. At Templeton, where Romney-Corrièdale crosses displayed relatively little hybrid vigour, probably reflecting the recent Longwool ancestry of Corrièdales, the average superiority of first-crosses involving the Dorset over the corresponding parental breeds averaging 13%, 6%, 10% and 3% respectively. The lower (arrowed) ends of the lines shown in Figures 1 and 2 indicate the expected performance, under a genetic model in which heterosis is proportional to heterozygosity, of two breed synthetics derived by interbreeding (without selection) each of the crosses studied. The projected lengths of these lines along the X and Y axes thus indicate half the heterosis for fleece weight and weight of lamb weaned, respectively, and further emphasise the importance of heterosis to meat production.

As noted by Nitter (1978) heterosis has been observed to vary with age and environment in addition to breed and the trait under study. Important declining age trends in live lamb production per ewe were observed by Ch'ang and Atkins (1982) for Doreset Horn x Corrièdale crosses and invoke caution in the interpretation of early experimental results.

Terrill (1982) discussed the tendency in U.S. results for heterosis to appear most useful under more difficult conditions, e.g. at Beltsville where most of the breeds kept are better adapted to a more temperate climate than prevailing hot humid conditions. Hohenboken et al., (1976) also reported that crossbred matings were more productive of lambs than purebred matings under an intensive management regime which reduced overall productivity compared with extensive grazing on hill pastures. Studies in pigs have demonstrated increased growth rate and feed conversion superiority of crossbreds over purebreds under restricted in contrast to ad lib. diets (Sellier, 1976). If heterosis can cover up or mask the effects of a difficult environment, it offers increasing promise in meeting the vagaries of fluctuating seasonal conditions as sheep production intensifies or moves to more difficult environments due to competition for limited resources and market outlets.

Wiener and Hayter (1975) argue that heterosis may sometimes be observed if one of the purebreds is unable to realise its full potential because of some environmental limitation or disease situation - i.e. a different environment may produce a different result implying the existence of genotype-environment interaction in the observed manifestation of heterosis. The topic has also been discussed by McGuirk et al. (1978) and used to explain the high heterosis observed in crosses among Bos indicus and Bos taurus breeds of cattle (Gregory and Cundiff, 1980). Genotype x environmental interactions arising from competition
between genotypes run together are also of concern especially when results are to be extrapolated to commercial circumstances in which the genotypes would probably be managed separately (Clarke and Meyer, 1982). Ch'ang and Atkins (1982) highlight an important genotype x environment interaction arising in a comparison of Border Leicester x Merinos, Dorset x Merinos and Merinos under autumn and spring joinings (Fogarty, 1978). The results indicate a much more pronounced effect of spring joining on reproductive performance for the Border Leicester x Merino than the other two genotypes.

The general conclusion from these trials is that while first-crosses tend to show an important superiority over purebreds, especially for survival and reproduction and under sub-optimal production conditions, this advantage is largely unpredictable for particular breeds and systems of production and merits eventual specific study of crosses among the most promising breeds available to the industry.

Interbred Generations

Wiener and Woolliams (1982) compared and interbred Scottish Blackface, Cheviot and Welsh Mountain sheep and their crosses, as well as crosses made among inbred lines derived from them over several generations. Inbreeding produced profound changes in several aspects of performance but did not accord well with expectations when its effects in purebreds and crossbreds were compared. This combined with the poor general relationship between F1 and F2 heterosis and between heterosis and inbreeding depression suggested that non-allelic interaction may be an important source of variation in performance (Kinghorn, 1980; Sheridan, 1981).

McGuirk et al. (1978) compared their estimates of hybrid vigour for hogget traits in Border Leicester x Merino crosses with those obtained by Pattie and Smith (1964). They agreed quite well despite the different methods of estimation. Large estimates of hybrid vigour for ewe reproductive traits were however obtained by Pattie and Smith (1964) and in other comparisons of F1 and F2 performance (Nitter, 1978). Wiener and Hayter (1975) note in their trials that heterosis for maternal performance present at the F1 stage appears to have vanished in the F2. Similar trends were apparent for Border Leicester x Romney crossbreeds at Whatawhata (Hight and Jury 1970a, 1970b, 1971, 1973). Based on a simple genetic model which only includes average genetic and heterotic effects for individual performance of their breeding ewes, Clarke (1982a) estimated heterosis for weight of lamb weaned as 58% of the predicted mid-parent value. Under the same model it was 39% for weaning rate (lamb weaned per ewe exposed). Including earlier results from a first-backcross generation Clarke (1962), in a model which includes average breed, heterotic and recombination loss effects for individual performance, gave an estimate for recombination loss of 17% of the predicted mid-parent mean. The consequential estimate of individual heterosis for weaning percentage as a trait of the ewe was 12%, considerably less than estimated from models which ignore effects of gene recombination (Nitter 1978, Clarke 1982a). However, comparison of F2 and F3 performance suggests that heterotic and recombination loss terms for maternal effects should probably not be ignored (e.g. 2(F2-F3) = h_{M} r_{M} = 0.1 lambs/ewe at Whatawhata).

Dickerson's early (1977) summary of data since published by Oltenacu and Boylan (1981) also provides evidence of adverse gene recombination effects for litter size at birth and weaning, F2 generations exhibiting a large decline over the average of the parental and F1 generations, at least twice as large as those
shown by the first backcross generations. Based on an analysis of three-breed-cros
lambs produced by crossbred sires in comparison with an expectation based
on all corresponding two-breed-cross lambs, Teehan et al. (1979) found small
but also unfavourable estimates of recombination loss. The results of current
U.S. studies (Cundiff, 1982) are awaited with interest.

In general terms the studies reviewed re-affirm the superior performance
displayed by first-crosses but give little confidence to the prediction of inter-
bred performance except in situations where average genetic differences between
the breeds being crossed are relatively large.

METHODS OF BREED UTILISATION

In contrast to previous reviews, emphasis is given here to important indus-
try constraints and operational factors influencing the feasibility and likely
acceptability of different crossbreeding systems for sheep production.

Specific Crossing

Where maternal heterosis is important, the three-way cross of a superior
sire breed to superior first-cross ewes has both genetic and operational advan-
tages. In addition to utilising hybrid vigour, the system allows the breeds
chosen as parents of the slaughter lamb to complement one another to better
meet production objectives. By appropriate choice the good features of breeds
can be combined and genetic antagonisms between parental and progeny performance
avoided to some degree (Moav, 1966; Robertson, 1971; Sellier, 1976). Of con-
siderable genetic importance to long-term industry stability is the specialisa-
tion of selection objectives for dam-line and terminal-sire breeds that specific crosses
Accordingly, lamb growth, carcass yield and carcass quality assume increased
significance in terminal sire compared to breeding ewe breeds, although as shown
previously, sire effects on survival and wool production in the young slaughter
lamb generally cannot be ignored.

For sheep the extent of specific crossing is severely limited in comparison
with more fecund species by the low "excess fertility" of the breeding popula-
tion (Robertson, 1971). As demonstrated by Nitter (1978) this depends upon the
average lambing and death rates of the ewes, their length of productive life and
the extent of culling among young flock replacements. Often less than 50% of
the total sheep population can comprise crossbred ewes (Nitter, 1978; Clarke,
1982a). The remainder must be mated to rams of their own breed to generate
purebred replacements for the population. Improved "excess fertility" and a
spread in the costs of producing young flock replacements can often be achieved
if the effective productive life of proven breeding ewes is extended an extra
year or two by moving them to easier conditions.

Industry-wide stratification often already exists but otherwise may be
slow to evolve without major direct incentives to individual producers based on
anticipated overall benefits to the industry as a whole. Specialised export
lamb producers must either have confidence in the genetic improvement programmes
of the breeders from whom they purchase terminal sires or breeding ewes, reflect-
ing this confidence in the prices they are prepared to pay for breeding stock,
or they must undertake this specialisation within their own farms. In the
latter case the costs of specialisation are reflected in an increased complexity
of their on-farm breeding programme. This will often be greater than on an
industry-wide basis because the benefits of scale, for economic or genetic rea-
sons, may not be able to be exploited to the same degree (e.g. costs associated
with increased inbreeding and reduced selection pressure in flocks of small

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rather than large size). Breed variation in adaptation to environment can be a further reason favouring industry-wide rather than on-farm specialisation, while individualism arising from different attitudes towards specification of appropriate breeding goals and methods of achieving them may act in either direction.

New Synthetic Breeds

An important operational advantage favouring the development of new synthetic breeds over other methods of breed utilisation is the ease with which selection practices may be established. Indeed, as discussed by Clarke (1982b), the development of the new breed may itself encourage an awareness and involvement in performance recording and selection for both the new breed and its competitors. Theoretical predictions of enhanced selection response in new synthetic breeds suffer from lack of knowledge of the precise genetic circumstances prevailing (Hill, 1971). Phenotypic and genetic parameters have been estimated for the Dam Line recently developed in the U.K. (Martin et al. 1980 and 1981) and, as expected (Hill, 1971; Lopez-Fanjul, 1974), fall in line with previous published estimates.

An additional operational advantage of synthetics is the ease with which a uniform management system may be applied to the flock as a whole once parental genotypes have been replaced by newly-developed crossbreds. Mating management also becomes simpler at this stage. Breeds chosen for use in development of synthetics need, however, to be compatible or complementary with respect to their average genetic merit for all important production traits.

Major Gene Effects

A variation of synthetic breed formation involves the introduction of a strongly inherited characteristic (e.g. polledness) into an existing breed by backcrossing and selection. Dry (1965) has discussed the benefits of this approach with reference to the N-gene which now forms the basis of the Drysdale breed. Other specialty carpet wool breeds also depend on the presence of a single major gene (Wickham and Rae, 1977).

Similar Mendelian approaches may prove important for development of improved fecundity breeds by crossbreeding with Booroola Merinos, particularly if simple methods for identifying young rams of different genetic constitution can be found. Despite this present limitation, progeny testing programmes in N.Z. have already identified a small number of Merino rams apparently homozygous for the gene and from which large numbers of homozygous rams could be bred. Such rams should be capable of increasing lamb production by 50%. It will be relatively straightforward to transfer the gene to other breeds by backcrossing and selection since this requires that crossbred females be selected according to whether they carry the gene, using ovulation or litter size records, and males on the attributes of the breed receiving the gene, there being no need to recognise male carriers until sufficient backcrossing has been done. At this stage controlled dissemination can start as soon as homozygous rams have been identified using, at present, progeny testing on daughter performance. Smith and Webb (1981) have discussed further breeding strategies to exploit a major gene.

Rotational Crossbreeding

This has the advantage that only males are introduced into a system which produces its own female replacements. Both are particular advantages if disease problems are important. However, the males must come from flocks with appropriate and effective selection programmes. In addition, since each breed contributes on average to the same extent on the sire as on the dam side of the cross, there
is little opportunity for optimum genetic balancing of the individual and maternal effects on performance (Gregory and Cundiff, 1980). Consequently, selection needs to be for both ewe and lamb performance traits within each of the breeds and there is less opportunity for breed specialisation to take place in contrast to specific crossbreeding. Furthermore, since the genotypes of the progeny are 50% determined by the breed of sire used last, there is less uniformity between generations and hence less opportunity for genetic adaptation to the environment, or vice versa especially when generations overlap. Despite these managemental problems rotational crossbreeding is able to utilise considerable heterosis for both individual and maternal effects, depending upon the number of breeds involved, while in addition, recombination loss is kept low since only female parents are crossbred.

FUTURE CONSIDERATIONS

Although little is known about many of the variables which determine cost/benefits of breed utilisation, increasing information on per head production from well designed breed comparisons is allowing crossbreeding practices to be better evaluated and modified. For many production systems however, it will always be difficult to make effective breed comparisons simply because conditions vary so much from one farm to the next or because so many of the important costs of production are difficult to assess and ascribe to appropriate paths in the chain of production leading to the final product. As stressed by Carter (1976), breed evaluation is a step-wise process which gradually intensifies as information is gained and used to discriminate among alternative breeds, crosses and management systems. This is illustrated by current attention to recombination loss as recent crossbreeding studies progress beyond initial generations.

Nitter (1978) studied various crossbreeding systems for sheep using average estimates of heterosis for meat production but ignoring recombination loss and average breed differences (other than in terminal sires) as well as the effects of selection and wool production on productivity. In general, his predictions showed that the superiority of crossbreeding over straightbreeding would depend largely upon the extent to which crossbreeding strategies were able to exploit heterosis in maternal performance in addition to heterosis in lamb traits. They nevertheless served to indicate areas likely to be rewarding of more detailed research study.

High estimates of hybrid vigour for breeding ewe traits suggest a future role for rotational crossbreeding for better exploiting heterosis and perhaps also better avoiding the effects of recombination loss. Farmer experience with rotational crossbreeding is sadly lacking and gives little meaningful insight into its operational problems. The fact that Romneys, Coopworths and Perendales are often farmed in N.Z. under similar farming conditions suggests that breed complementation and adaptation to local conditions may not always be important. Establishing effective on-going breed improvement programmes could however be a problem (McGuirk and Bourke, 1978) if progress from selection were limited by small flock size or poor reproductive performance unless cooperative breeding improvement strategies (Rae, 1977) were instituted.

On the basis of the considerable superiority of crossbreds over straightbreds for lamb production in the U.S., Terrill (1982) advocates a system of continuous multibreed crossing using crossbred rams. The aim is to establish a high proportion of crossbred ewes in the industry, on the expectation that the gains from heterosis would more than counterbalance any loss of additive merit in up to three-or four-breed cross lambs. The system is also seen as one which is suited to the exploitation of Finnsheep.
Many workers have discussed, in general terms, alternative crossbreeding strategies (Cundiff, 1982). Few specific studies have been conducted which take joint account of the effects of selection and of other important operational considerations affecting costs and especially the food costs of animal production. For beef cattle, computer simulation studies of crossbreeding systems have been undertaken by Cartwright et al. (1975) and Notter et al. (1979) and are reviewed by Gregory and Cundiff (1980). Bennett et al. (1982) have also recently simulated the effects of heterosis on costs of pork production. Similar studies are urgently needed for sheep.

Many workers have argued that breed or crossbred advantages might at times be offset by the lower stocking rate required by heavier animals. Atkins (1980), for example, showed that the percentage difference between Border-Merinos and Merinos was similar for weaning percentage and metabolic body size. Coop and Clark (1965) previously addressed this question for Border-Romneys in N.Z. On the basis of productivity per unit of metabolic body size, the combined wool and lamb superiority of F1 Border-Romneys over Romneys has ranged from 6-10% in N.Z. trials, the F2 and F3 generations being closer to Romney levels (Clarke and Meyer, 1982). Similar approaches have been used by workers in other countries (Smith et al., 1979). Most assume a common relationship between body weight and feed consumption for all genotypes and do not allow for breed differences in efficiency of forage harvest relative to seasonal patterns of forage production (Carter, 1982). There is an urgent need for factual information on such food related costs in view of the high proportion they make of total production costs under pastoral grazing (Carter, 1982) where so much of the world's sheep production takes place. The difficulties involved in estimating the net efficiency of alternative breeds and strains over the wide range of locations and production systems in which sheep are kept does not lessen the importance of this research if sheep are to survive as effective convertors of low-cost forage to high-quality protein for human consumption.

The world's breed resources are still at a very early stage of evaluation. Many appear to be threatened by a frequent assumption that the low apparent productivity of indigenous breeds should be improved by introduction of exotic genotypes (Baker, 1980). There seems little doubt that native breeds may often be particularly well adapted to survive and reproduce under particularly harsh local conditions even though little is known of the physiological basis to such adaptations (Slee, 1981). The recent SABRAO Workshop on Animal Genetic Resources in Asia and Oceania concluded that greater attention be given to improving the identification, documentation and evaluation of native breeds and strains. It recognised that a high proportion of total human food requirements is often produced from such genotypes and that the animals are also adapted to the socioeconomic conditions of the village farmer and his way of life. Breed adaptation to easy-care methods of farming are of increasing significance as farming costs rise. Uncertainties as to future requirements may justify breeding for currently unpopular or unprofitable objectives or at least maintaining genetic diversity through conservation of specialised strains with unique attributes as an insurance for possible future needs (Rae and Land, 1980).
SUMMARY

Improved knowledge of breed resources is providing greater understanding of their future role. Precise utilisation through crossbreeding gives flexibility to animal production by exploiting average genetic differences among breeds and hybrid advantages in their crosses, often allowing antagonisms within or between sheep farming costs and returns to be reduced. Development of new synthetic breeds to better exploit variation in meat, wool production, costs or scope for their joint improvement could in the future offer an even greater array of breeds for specific purposes. Improvement of fecundity using alternative breeds from various parts of the world, is likely to be of particular importance. High estimates of hybrid vigour, especially for reproductive performance, and under difficult conditions, suggest increased future application of more specialised crossbreeding strategies particularly if genetics benefits from improved performance can be obtained without marked increases in production costs many of which are very poorly known. Information on the comparative economic efficiency of different breeds apparently suited to particular management circumstances is sadly lacking. Research studies on the comparative food costs of genotypes of different mature body size are especially urgent.

RESUMEN

El aumento del conocimiento de los recursos raciales está proporcionando una mayor comprensión de su papel futuro. La utilización precisa del cruzamiento da flexibilidad a la producción animal al utilizar las diferencias genéticas medias entre las razas, y las ventajas del híbrido en sus cruces, frecuentemente cuando deben reducirse los antagonismos existentes dentro o entre los gastos e ingresos de la cría ovina. El desarrollo de nuevas razas sintéticas para explotar mejor la variación en la producción de carne y lana, los costes de producción o su mejora conjunta podría ofrecer en el futuro estrategias cada vez mayores aplicables a las razas con propósitos específicos. La mejora de la necesidad utilizando razas alternativas de varias partes del mundo parece ser de particular importancia. La elevada estimación del vigor del híbrido, especialmente para los rendimientos en la reproducción, bajo condiciones difíciles, sugieren aumentar la aplicación futura de mayores posibilidades de cruzamiento, particularmente si los beneficios genéticos del rendimiento mejorado pueden obtenerse sin aumentar marcadamente los costes de producción, muchos de los cuales son pocos conocidos. Falta notoriamente información sobre la eficacia económica comparada de las diferentes razas aparentemente escogidas para circunstancias particulares de manejo. Los estudios de investigación sobre costes comparados de la alimentación en genotipos de diferente época de madurez y tamaño corporal son especialmente urgentes.
REFERENCES


