
CHAPTER 13

Marker-assisted selection in sheep and goats

Julius H.J. van der Werf



SUMMARY

Sheep and goats are often kept in low input production systems, often at subsistence levels. In such systems, the uptake of effective commercial breeding programmes is limited, let alone the uptake of more advanced technologies such as those needed for marker-assisted selection (MAS). However, effective breeding programmes exist in a number of countries, the largest ones in Australia and New Zealand aiming for genetic improvement of meat and wool characteristics as well as disease resistance and fecundity. Advances have been made in sheep gene mapping with the marker map consisting of more than 1 200 microsatellites, and a virtual genome sequence together with a very dense single nucleotide polymorphism (SNP) map are expected within a year. Significant research efforts into quantitative trait loci (QTL) are under way and a number of commercial sheep gene tests have already become available, mainly for single gene effects but some for muscularity and disease resistance. Gene mapping in goats is much less advanced with mainly some activity in dairy goats. Integration of genotypic information into commercial genetic evaluation and optimal selection strategies is a challenge that deserves more development.

INTRODUCTION

The benefits of marker-assisted selection (MAS) to sheep and goat breeding programmes depend on a number of conditions that are relevant for most breeding programmes across species. These conditions include the existence of a genotype test predicting phenotypic differences, the economic value of these differences and the value of the genotypic information within the breeding programme. The value of genetic information will depend heavily on the socio-economic context of the breeding programme and the production system. In a technical sense, the value of this information is basically driven by the increase in selection accuracy resulting from knowledge of genotypes, which in turn will differ between animals from different age classes. In particular, the relative increase in selection accuracy of the youngest selection candidates will be critical to the value of MAS. However, technical arguments about increased selection accuracy are of little value if these selection criteria are poorly developed or accepted within the production system.

The application of new technologies such as MAS in animal breeding programmes therefore depends not only on a number of technical aspects associated with increased rates of genetic improvement, but also on the commercial structures of the industry. For example, the uptake of MAS in breeding programmes depends on the willingness of breeders to invest in genotypic information, and their ability to turn this into knowledge that helps them improve their commercial breeding activities. A basic understanding of breeding programme characteristics, the possible role of genetic information within these programmes, and the commercial relationships among the different players are needed to assess the

value and predict the application of MAS in breeding programmes. These commercial relationships are distinctly different in sheep and goat breeding programmes from those in the more intensive animal industries, and the application of MAS will therefore be different. For example, 96 per cent of the world goat population is kept by smallholders in developing countries, and genetic improvement programmes are rare (Olivier *et al.*, 2005).

The purpose of this chapter is to describe the use of MAS in breeding programmes for sheep and goats and the likely rate of uptake of this technology in these species. It begins by characterizing such programmes and describing and comparing existing programmes. MAS is most useful for traits that cannot be improved easily by phenotypic selection, either because they are difficult to measure on young animals (before sexual reproduction), or because of low heritability. Therefore, breeding objectives are discussed in general terms and the traits that are particularly suitable for MAS are identified. Based on some general well-known advantages of MAS, its possible role within breeding programmes can be predicted and examples of these are provided. Examples of marked genes are then described and an overview given of the status of “gene discovery” and gene mapping projects in sheep and goats. The chapter concludes by describing cases of using this information in actual breeding programmes. Some gene tests are based on actual functional mutations, many of which do not affect quantitative traits that are generally targeted in breeding programmes. Although, the term “MAS” should be replaced in some cases by “genotype assisted selection” (GAS), the term MAS is used loosely to refer to all selection based on genotypic information. It will become clear that

currently most real applications of MAS for sheep and goat breeding are based on research projects and therefore subsidized. However, the first commercial applications are now also emerging. The main requirements for a successful commercial and long-term application of MAS in sheep and goat breeding are discussed and illustrated based on examples.

MAS applications are often illustrated or simulated for pure breeding programmes. However, MAS could be particularly useful in crossbreeding programmes where desirable genotypes in unfavourable backgrounds are introgressed into productive local breeds with overall better breeding values. The opposite is also possible, where disease resistance genes of local breeds are specifically targeted in upgrading programmes with imported stock with higher productivity being crossed to local breeds. Crossbreeding and introgression programmes are discussed and, as sheep and goat production is relatively predominant in developing countries, particular attention is given to breeding programmes for low to medium input production systems.

CHARACTERISTICS OF SHEEP AND GOAT BREEDING PROGRAMMES

Breeding structures

Breeding programmes for sheep and goats generally operate within an industry that is based on low levels of resource inputs, i.e. low levels of feeding and low labour costs on a per animal basis. Goat production takes place largely in developing countries where selective breeding based on performance recording is often absent. A more substantial proportion of sheep production is found in developed countries such as Australia, France, New Zealand, South Africa and the United Kingdom. These systems are also predominantly pastoral-based and extensive

in nature. An FAO working group report (Hoste, 2002; Olivier *et al.*, 2005) made the following distinction between production systems and the opportunities within them for breeding programmes: 1) subsistence-based production, among the world's poorest, with limited market development and limited inputs and scope for genetic improvement; 2) market-based production, with better developed markets targeting urban populations, higher input levels and more specialized production systems, with scope for genetic improvement depending on cost of inputs and also on skills and information literacy of breeders and producers; and 3) high-input production, with further specialization, emphasis on increased land and labour efficiency, and much more concern for food quality, food safety, animal welfare and the environment. Most of the world's goat production as well as many of the sheep systems would fall into the first category, whereas sheep production in developed countries would mainly fall into the second category, with some of these working towards the third category.

Sheep and goat breeding programmes are characterized by a flat breeding structure, meaning that compared with intensive livestock industries many operations participate in genetic improvement, thereby forming a wide base for the nucleus breeding sector. Reproductive levels of breeding animals, especially males, are relatively low compared with other species. In such a system, the multiplication factor, i.e. the number of commercial expressions resulting from investments in improved genotypes in the breeding nucleus, is relatively low. This makes it more difficult to introduce new technologies and justify large investments in improving individual animals. However, like other breeding programmes, there remains

a significant return on overall investment in genetic improvement. Also, in some more advanced sheep breeding programmes, the use of artificial insemination (AI) and across-flock evaluation has boosted the use of high profile rams and raised the value of individual breeding animals.

The main investment in breeding programmes is for performance recording. The extent of trait measurement is often quite closely aligned with the intensity of the production system. Input levels for sheep production vary, depending on breed type and market. In Australia, for example, there is a significant difference between wool producing Merino sheep that are kept extensively in harsh environments, and more intensive lamb production systems that are found in higher rainfall areas or on irrigated land. The proportion of breeding flocks for which objective trait and pedigree measurements are undertaken is relatively much higher in the Australian terminal sire breeds.

Selection takes place within the breeding studs. AI is common in the stud breeding sector, enabling the genetic linkage of flocks. There are breeder groups with organized progeny testing of young sires across flock programmes. In Australia, a national genetic evaluation system known as “Lambplan” has driven genetic evaluation for terminal sires and maternal breeds across flocks for more than a decade. Breeders as well as ram buyers are increasingly basing their ram assessment on estimated breeding value (EBV) or dollar index value. Such a system gives breeders incentives to invest in trait measurement and to create genetic links between their flocks, otherwise it would be difficult for a ram to rise to the top of the across-flock EBV list. Hence, there is increasingly an exchange of genetic material between flocks, mainly through the use

of AI. Obviously, such a breeding structure would be more conducive to breeders investing in gene marker technology.

By contrast, the Australian Merino industry has had a much lower proportion of breeders taking up trait and pedigree recording. The industry is more traditional and selection is most often based on visual assessment. While this might be due partly to the sector being more extensive, AI has been commonly used in the Merino stud sector and top Merino rams have always been sold for high prices. Therefore, the extensive nature of the industry does not fully explain the lack of investment in performance recording. The traditional nature of the industry that has hampered the uptake of quantitative genetic principles is also the result of socio-economic factors, with wool producers being traditionally a prominent and relatively wealthy social class. The lamb industry has long been the wool person’s “poor brother”, but this lack of status has accelerated innovation with the introduction of new approaches such as formal recording and across-flock evaluation. Hence, economic as well as social and cultural reasons may explain why sheep breeding programmes have different levels of sophistication in terms of recording, genetic evaluation and across-flock selection.

BREEDING PROGRAMMES AND TRAITS TARGETED

Meat sheep

Large-scale genetic evaluation programmes for sheep are found in Australia, France, New Zealand, South Africa and the United Kingdom. In all of these, performance recording for meat traits is well advanced, with not only weight traits measured, but also traits related to carcass quality such as body fat and muscle (based on ultrasound

scanning and in some cases computer tomography [CT] scanning), disease (mainly resistance to internal parasites) and reproduction. The national evaluation system in Australia (“Lambplan”) now has about 120 000 new animals from about 450 flocks recorded each year for terminal sire breeds and maternal breeds (A. Ball, personal communication). Performance recording takes place only at the stud level, which in a sense is a dispersed nucleus, and a large proportion of the genetic basis of the commercial population stems from these recorded flocks. The proportion of pedigree recorded individuals is high at the stud level, allowing best linear unbiased prediction (BLUP) of EBV. In New Zealand, a similar programme exists (“Sheep Improvement Limited” [SIL]), in which pedigree and performance records are registered with genetic service providers and the information “retailed” back to the breeders. SIL enters more than 250 000 new animals per year from some 750 recorded flocks, all pedigree recorded, and has a database of more than 5 million animal records. Across-flock EBVs are estimated for a proportion of these. In the United Kingdom, about 50 000 breeding ewes and their lamb records are recorded every year from 37 different breeds, and indices have been developed for terminals and maternal (“hill”) breeds (Conington *et al.*, 2004). Across-flock genetic evaluation programmes for meat sheep breeds exist also on smaller scales in France, Norway and South Africa.

Most breeding programmes for meat sheep focus on weight traits, and ultrasound scanning is commonly used for fat and muscle traits. Reproduction traits are recorded as numbers of lambs born and weaned. Selection for resistance to internal parasites can be based on faecal worm egg counts (WECs) associated with natural

challenge in the field, e.g. in Australia and New Zealand, and this has been shown to be reasonably heritable in Merino sheep (e.g. Khusro *et al.*, 2004). EBVs for WEC are produced for an increasing number of flocks in Australia and New Zealand.

The traits that would most obviously benefit from MAS in meat sheep would be traits related to carcass and carcass quality, reproduction and disease resistance. Ultrasound measurements are currently used to predict carcass fat and muscling. However, genetic correlations with traits measured on carcass are only moderate (Safari, Fogarty and Gilmour, 2005) and specific meat quality attributes such as tenderness and colour might not be well captured by current measurement. Carcass traits are prime targets for MAS as they cannot be measured on breeding animals and progeny or sib testing would be needed as an alternative. Reproduction traits as well as maternal behaviour and ewe survival are also good MAS targets as they are sex limited and are only expressed after the first round of reproduction. Disease resistance traits are generally hard to measure under uniform conditions and would also greatly benefit from MAS.

Wool sheep

Breeding for and recording of wool traits is limited to a few countries. The largest across-flock scheme is found in Australia (mainly for the Merino breed), and smaller genetic evaluation schemes are run in New Zealand, South Africa and South America (Merino and Corriedale). In Australia, the proportion of breeders participating in formal recording and genetic evaluation is smaller for wool than for meat sheep. However, the Merino industry is very large, constituting the vast majority of the Australian flock that consists of about 100 million sheep. By

the end of 2005, a new single system for a national across-flock genetic evaluation of Merinos had been introduced in Australia, combining data from previously separate schemes. The number of animals performance recorded per year is growing rapidly, with about 100 000 new animals now being entered annually.

Wool production efficiency is mainly determined by fleece weight and wool quality. Wool quality traits are mainly fibre diameter and staple strength, and these are economically much more important for fine wools. Staple strength is more expensive to measure, but has a high correlation with the coefficient of variation of fibre diameter, which is therefore a good predictor. Wool traits have generally high levels of heritability, especially fleece weight and fibre diameter.

Reproductive rate in wool sheep has been hard to select for as pedigree recording has been limited and the heritability is low. Moreover, genetic improvement of reproductive rate has been less important for wool production because of the positive net economic benefit of wool producing breeding females. However, with an increasing meat/wool price ratio, the situation is changing and reproductive rate is currently becoming more important. Also, meat attributes of Merino sheep are now receiving increased attention, including measurements of body weight at different ages, fat depth and eye muscle depth (ultrasound scanned).

In pure wool production systems, MAS would be expected to have limited benefit for wool production traits because of their high heritability and the ability to measure the traits before the age of first selection. MAS for reproductive traits and mothering ability would be more beneficial because of low heritability and sex-limited recording.

Parasite resistance is becoming a trait of greater economic importance due to the development of resistance to all the major classes of anthelmintics used and the lack of new anthelmintic classes being developed. Host resistance to internal parasites is particularly poor in the Merino breed. The trait can be selected for using field records of WEC. EBVs are being produced for this trait and genetic progress is being achieved. However, the procedure is laborious and there is also some concern about uniformity of measurement and trait definition, as well as the existence of different species of parasites in different regions. Various studies have looked at genotype \times environment interactions for parasite resistance and, although some interaction exists, relatively high correlations (~ 0.8) were found between breeding values in different environments, when environments were defined either through worm type (McEwan *et al.*, 1997) or by high and low flock averages for WEC (Pollot and Greeff, 2004). In any case, many of these trait attributes make parasite resistance a good target for MAS. Identifying QTL for parasite resistance might also shed more light on the biology of immunity, and possibly help to find other modes of improvement.

Feed efficiency, and particularly maternal efficiency, are important determinants of pastoral production systems (Ferrell and Jenkins, 1984) and genetic improvement would benefit from MAS because of the cost of their measurement. However, feed availability and feed costs are quite variable within and between years, and the ability of sheep to cope with harsh environments and periods of drought is perceived by industry as being of greater importance. Hardiness and ewe survival are not well defined characteristics and are not normally measured in breeding programmes.

Ewe fitness and adaptation are often used as the main argument for the existence of genotype x environment interaction in wool production, inhibiting the exchange of genetic material among regions. Carrick (2005) found moderate to high genetic correlations between wool production traits in flock groups differentiated by their phenotypic means for a range of production traits. Discovering QTL for fitness and survival traits in different environments would be useful, but these are unlikely to be found unless the traits themselves are clearly defined and measured.

Dairy sheep

Dairy sheep are predominantly found in the Mediterranean region with both milk and meat production being economically relevant traits to farmers. A great variety of breeds are being targeted in selection programmes for the improvement of milk yield and milk composition but the importance of functional traits such as udder characteristics and mastitis susceptibility is increasing (Barillet, 1997; Barillet, Arranz and Carta, 2005). Genetic improvement for dairy traits, being sex-limited and measured after the first offspring are born, would particularly benefit from MAS.

Goats

Most goat farming systems focus on meat production (about 80 percent), with more emphasis in developed countries on dairy goat production (Olivier *et al.*, 2005) and fibre production (cashmere, mohair). In dairy goat breeding, the most developed breeding programmes are found in France and are based on a strong goat cheese market. Based on AI and milk recording, Caprigene France runs selection schemes for the Saanen and Alpine breeds, with 300 000 goats in 2 500 herds being recorded

for milk traits. Dairy goat production is also recorded on smaller scales in Italy, Norway and Spain, with no more than a few thousand animals recorded in other countries (Montaldo and Manfredi, 2002). The main traits in dairy goat production are milk yield and protein and fat content of milk. Being sex-limited and measured only after first production of progeny, these traits would benefit from MAS.

Goat meat production is widely spread throughout the developing world but there are few breeding programmes of any significance. Genetic evaluation for Boer goats and other meat breeds is taking place in Australia and South Africa with weaning weight usually being the main trait measured. Ultrasound measurement of fat and muscle traits is less common in goats, while reproductive traits have had less attention, possibly because of their low heritability and multiparous nature. There are few studies concerning resistance to internal parasites in goats (Olayemi *et al.*, 2002), but these seem to indicate that faecal WECs could be a similar selection trait as in sheep. However, the trait is hard to measure and there is no systematic recording and evaluation in breeding programmes.

DEVELOPMENT OF SHEEP AND GOAT GENOME MAPS

Several key publications have reported progress on the linkage map of the sheep genome based on an international mapping flock developed in New Zealand (Crawford *et al.*, 1995; Maddox *et al.*, 2001). The latest sheep linkage map (version 4.3) comprises 1 256 gene markers mapped to unique locations (Maddox, 2004) and most genomic regions are well covered with a maximum gap of 20 cM. However, there are quite a number of markers of low quality, so a typical genome scan would leave a number

of gaps. Most of the markers are microsatellites. The total number of sheep loci listed in the ARKdb database (<http://iowa.thearkdb.org>) contains more than 2 000 markers, but many of these are not on the linkage map. The development of the sheep genome map runs somewhat behind developments for other livestock species because of substantially lower investments. Nevertheless, at the DNA level where the sequence can be aligned, there is a ~90 percent homology with the cattle sequence and through gene coding regions ~96 percent, and the sequencing of the cattle genome will therefore greatly enhance the development of the genome map in sheep. There is generally good agreement between sheep and cattle maps, with 598 mainly anonymous common microsatellite loci, i.e. gene markers can be linked to a comparative map. Based on sequence information in other mammals (mainly cattle) and sheep GeneBank sequences, comparative mapping can be used to construct a predicted sheep map. This can be accessed from the Australian Gene Mapping Web site (Maddox, 2005a). The number of single nucleotide polymorphism (SNP) markers in sheep is still very low, but with the cattle sequence known and with an international collaborative sheep bacterial artificial chromosome (BAC)-end sequencing project under way, it is expected that there will be a large number (~16 000) of SNPs available for sheep towards the end of 2006. This will form a set of markers that would allow high-density genome-wide scans.

The goat map is more sparse than the sheep map and contains about half the number of markers known in sheep: 731 loci with 271 genes and 423 microsatellites (<http://locus.jouy.inra.fr/>). The last published linkage map for goats contains only 307 markers (Schibler *et al.*, 1998),

with coverage of the whole goat genome being far from complete. Although the sparsity of the sheep map makes it difficult to develop a good homology between the maps, about two-thirds of the mapped goat markers can also be linked to the sheep map (Maddox, 2005b).

QTL AND GENE MAPPING

An excellent overview of mapping experiments in sheep can be found on the Australian Gene Mapping Web site (Maddox, 2005a), including references to identified QTL and genes. Successfully identified genes and QTL are related mainly to fecundity, disease resistance and meat quality.

Fecundity

Two genetic mutations have been reported for fecundity: the Booroola mutation: FecB on chromosome 6 (Wilson *et al.*, 2001; Mulsant *et al.*, 2001; Souza *et al.*, 2001) and the Inverdale gene: FecX on the X chromosome (Galloway *et al.*, 2000). The Booroola gene has a substantial additive effect on ovulation rate with each copy increasing this by about 1.5 eggs (i.e. scanned foetuses). The additional allelic effect of the Booroola mutation on litter size is about 0.8 to 0.9 lambs (Davis *et al.*, 1982; Piper and Bindon, 1982; Gootwine *et al.*, 2003) whereas a second copy of the mutation has a slightly smaller effect (0.4–0.6 lambs). The effect on number of lambs weaned is somewhat lower. The effect of the Booroola gene is often perceived as too large and the survival of twin and triplet lambs decreases substantially in extensive and harsh conditions, typical for many sheep flocks. For example, in the Australian Merino industry, the Booroola mutation is not seen as a desirable characteristic. However, the Booroola gene has been introduced in many sheep populations around the world.

The Booroola mutation possibly originates from the Indian Garole (Davis *et al.*, 2002) and, interestingly, the gene effect appeared to be smaller (0.6 lambs born alive) in an Indian introgression programme with Deccani sheep (Nimbkar, Pardeshi and Ghalsasi, 2005). This increase in litter size appears to be easily managed in shepherd flocks. A smaller effect would be more desirable for extensive production systems. It is not clear whether the reduced gene effect arises from a modification due to environmental effects or the genetic background. As the reproductive rate is a trait of high economic value, and due to the availability of a test for the actual gene mutation, Booroola remains a very interesting gene for MAS and marker-assisted introgression (MAI) programmes.

The Inverdale gene has been mapped to the X chromosome and has an effect of about 0.6 lambs per ewe lambing. However, the homozygous ewe is infertile. As carrier rams as well as non-carrier ewes need to be maintained in a crossbreeding system, using this gene in the industry is more complex. However, the 100 percent accurate test has made the use of this gene more manageable.

A number of other major genes for fecundity have been described by Davis (2005), but the molecular basis of these effects has not been formally described.

Disease

Internal parasites are the main cause of economic losses due to health problems in sheep and goat production systems. Although there is significant research under way to detect and map QTL for host resistance to internal parasites, there have not yet been any major breakthroughs in terms of detected polymorphisms in functional genes. Few QTL have been reported for

resistance to internal parasites (see review by Dominik, 2005) but not all results are reported in the literature. A major gene effect for resistance to *Haemonchus contortus* was found based on segregation analysis (Meszaros *et al.*, 1999) but this has not been confirmed based on gene markers. The problem of finding distinct QTL for resistance to internal parasites may be due to the complexity of the underlying biological mechanism as well as the difficulty of finding well-defined phenotypes that measure resistance.

Transmissible spongiform encephalopathy (TSE) is a prion disease like scrapie and is characterized by the accumulation of a modified form of a protein known as *PrP*. The *PrP* gene has been associated with variation in scrapie susceptibility in sheep (Moreno *et al.*, 2002), mice (Moreno *et al.*, 2003), and goats (Acin *et al.*, 2003). The gene only explains a proportion of the overall variation for increased resistance to scrapie. Commercial gene tests are available for the *PrP* gene mutation.

A causative mutation has been found for the Spider Lamb Syndrome. This is a relatively rare recessive skeletal disorder with the responsible mutation being assigned to chromosome 6 (Cockett *et al.*, 1999). A commercial test is available for this syndrome.

A gene test based on the *DQA2* gene that resides on the MHC complex (Hickford *et al.*, 2004) and predicts susceptibility to foot rot has been developed at Lincoln University in New Zealand. Thirty-one different alleles have been identified for *DQA2* and a gene marker test rating has been developed based on a susceptibility score of the two alleles of a genotype. There is a clear association between the test rating and the relative risk of contracting foot rot. A gene marker test has been available since

2001 and has been used extensively (over 40 000 tests).

The β -3 adrenergic receptor gene has been sequenced (Forrest and Hickford, 2000) and eight different alleles have been found. This allelic variation is significantly associated with increased risk of cold-related mortality of lambs.

Meat traits

The first causal mutation found for meat traits in sheep is the callipyge gene causing muscular hypertrophy. The gene has been mapped to chromosome 18 and the causative mutation has been identified. However, the trait is expressed in a rather complex manner, termed polar over-dominance; only lambs that inherit the callipyge mutation from their father but not their mother develop the trait. Several interacting genes are involved and the complete molecular basis of callipyge phenotypes has not yet been fully resolved (Freking *et al.*, 2002; Cockett *et al.*, 1996, 2005).

The Carwell gene somewhat resembles the callipyge gene, as it has been mapped to the same genomic region (distal end of chromosome 18) and it also affects muscling (McLaren *et al.*, 2001). However, the overall phenotypic effect is not exactly the same in that the Carwell gene affects only the *longissimus dorsi* and unlike the callipyge gene it has not been associated with a decreased tenderness if the meat is aged appropriately and neither does it seem to be affected by the parent of origin (Jopson *et al.*, 2001). The functional mutation of the Carwell gene, also known as the rib-eye muscling (REM) gene, has not yet been found but close markers in linkage disequilibrium with the putative gene are being developed in Australia, New Zealand and the United Kingdom. A commercial gene test termed “LoinMax”

was introduced towards the end of 2005 by Ovita in New Zealand.

A number of gene detection projects have resulted in significant QTL for muscle, fat and other carcass traits, but not all of these have been published, confirmed or fine mapped. A number of studies have reported on QTL for meat traits in sheep (Broad *et al.*, 2000; Walling *et al.*, 2004; Johnson *et al.*, 2005; McRae *et al.*, 2005) and there are probably some unpublished QTL being further developed. Some of these sheep QTL are based on related cattle genes, e.g. the myostatin gene for double muscling (Grobet *et al.*, 1997) and the thyroglobulin gene affecting intramuscular fat (Barendse *et al.*, 2004).

Wool traits

In a recent paper, Purvis and Franklin (2005) reviewed QTL for wool production traits and wool quality. Although wool traits can be measured easily and have high heritability, these authors suggested that research into certain wool production genes was still justified, for example, to break antagonistic correlations (between fleece weight and fibre diameter) or to target specific wool quality traits important for the processing of the product.

A few Mendelian (single locus) characteristics have been described for wool. There is a known mutation of the halo hair gene (HH1) causing extreme hairiness. This has been found in the New Zealand Romney breed and several lines have been developed for the production of “carpet wool” using this specific mutation. A recessive gene for hairlessness (*br*) has been described by Finocchiaro *et al.* (2003). Several QTL for wool traits have been published (see Purvis and Franklin, 2005 for an overview), but few of these have been confirmed. On the other hand, it is

probable that a number of QTL identified have not been published. It is likely that some of these wool QTL will be confirmed and available for gene testing over the next few years. Polymorphisms associated with candidate genes for the wool proteins keratin and sulphur have been described (Rogers, Hickford and Bickerstaffe, 1994; McLaren *et al.*, 1997) and seem to be associated significantly with fibre diameter and staple strength.

The genetic regulation of some forms of pigmented wool fibres has often been associated with the Agouti gene (chromosome 13) but this has proven to be a complex pattern of inheritance with several mutations seemingly involved (Smith *et al.*, 2002). More specifically, there appear to be two Agouti loci and at least two different polymorphisms (deletions). Currently, a genetic test for self coloured black wool is not yet available. Other pigmented phenotypes such as badger face and piebald also have a distinct Mendelian inheritance pattern (Sponenberg, 1997) but the molecular basis of these phenotypic variations has not been found.

Dairy traits

Research in dairy sheep has mainly focused on milk protein polymorphisms, in particular α 1-casein and β -lactoglobulin, but results have been inconclusive, unlike those in goats. Together with unfavourable allele frequencies, these results make it unlikely that these polymorphisms will be very useful in a MAS programme. Further QTL mapping work is under way, focusing on production and functional traits (Barillet, Arranz and Carta, 2005).

Other

The Horns gene has been found in sheep as described by Montgomery *et al.* (1996),

allowing improved selection efficiency for polled sheep.

Goats

Two goat genes have been well studied. Substantial mapping work has been dedicated towards finding a gene associated with Polled Intersex Syndrome (PIS), and the actual mutation for PIS has been described (Pailhoux *et al.*, 2005). Furthermore, the effects of the α s1-casein gene on milk solids content (protein, fat, casein, casein/protein ratio) have been described in French dairy goat breeds (Barbieri *et al.*, 1995) and the molecular basis has been unravelled (Yahyaoui *et al.*, 2003).

EXAMPLES OF SHEEP AND GOAT MAS BREEDING PROGRAMMES

There is little formal literature about actual applications of MAS in breeding programmes for any livestock species, let alone for sheep and goats. In fact, gene testing and MAS in sheep and goats have only very recently been introduced, and therefore the information compiled in this section is based mainly on information obtained from communication with colleagues in a number of countries (see Acknowledgements).

There are currently two types of MAS programmes. One is the use of gene markers in selection programmes within research projects. Usually the genotyping is subsidized and the purpose of the project is to create additional data for confirmatory studies of the QTL effect, or simply to obtain “proof of concept” where predictions based on simulation and modelling are being verified based on real data. In the other type of application, commercial gene testing is used. This is the scenario required for long-term and sustained use of the technology, but there are few

breeding programmes where commercial applications are viable. The basic condition is that ram breeders and ram buyers are prepared to pay for genetic information arising from genetic testing. This is more likely to happen in places where across-flock genetic evaluations already exist, combined with objective trait measurement and trait valuation in the form of indices. However, not all genetic information can be translated into dollar index terms and genetic testing is often valued beyond the existing index framework.

Experimental sheep MAS

The purpose of “experimental MAS” programmes is to demonstrate that genetic changes can be achieved based on genotype selection and thereby to encourage uptake of MAS by commercial breeders. Usually, the programmes are also designed either to estimate QTL effects more clearly, or to confirm earlier experimental results in industry flocks. Examples of such MAS programmes are:

- selection of sheep against susceptibility to scrapie, being conducted in France and the United Kingdom;
- the MAS Applied to Commercial Sheep (MASACS) Programme in the United Kingdom, coordinated by Oswald Matika from the Roslin Institute. The research team in this programme collaborates with commercial breeders. Three gene marker tests for muscling are being trialled in the first year and it is envisaged that a test for parasite resistance will be introduced in 2006. The three QTL are termed “Texel muscling” (chromosome 18), “Suffolk muscling” (chromosome 1) and “Charollais muscling” (chromosome 1) as described by McRae *et al.* (2005), and the tests will be applied within the respective breeds.

Commercial sheep MAS

Commercial gene testing in sheep is limited mostly to service providers in New Zealand, mainly Ovita and the University of Lincoln, whereas it is absent in goats. Details about gene tests can be found on the Australian Gene Mapping Web site (Maddox, 2005). Gene tests currently available are:

- Foot rot, a gene test commercialized by the University of Lincoln;
- Inverdale gene, through Ovita;
- Booroola gene, through Genomnz;
- Scrapie, (*PrP* gene), available through many companies (see Maddox, 2005);
- Carwell gene, available through Ovita as Loinmax;
- Texel Muscling gene (Chrom 2), available through Ovita as MyoMax.

None of these tests is currently integrated with formal genetic evaluation systems. Rather, gene test results and index values based on polygenic quantitative traits will have to be used separately, and holistic approaches are needed to devise selection rules. The gene tests for reproductive traits are not straightforward to use, while the Inverdale gene is only useful in a heterozygous state and requires specific crossing programmes. The Booroola inheritance model is more straightforward but the effect is too large for most management systems found in Australia.

It should also be noted that most of the commercial gene tests are for traits that are not captured by formal EBVs, and cannot be incorporated easily into existing EBVs, e.g. gene tests for disease traits such as scrapie and foot rot. In principle, the tests for muscle traits could be part of the EBV calculation, but from a ram marketing perspective it might be more useful to exploit the genotype information obtained more explicitly. Furthermore, the proportion of

breeding animals genotyped will be small in relation to the total number of animals evaluated based on phenotype, making an integration of genotypic information with the full evaluation procedure less sensible at this stage. Finally, service providers offering the genotyping results are often different from the service providers of EBV which inhibits a full integration of genetic information to the breeder.

In New Zealand, a significant and rapidly expanding part of the performance recording sheep industry already uses DNA parentage and the above-mentioned tests are now often provided as part of that system. At this point in time, DNA fractional parentage (Dodds, Tate and Sise, 2005) is included within the SIL system, but MAS EBVs for some of the above-mentioned tests (Inverdale, LoinMax) are only carried out on a stand alone basis, in the case of LoinMax since 1997.

Goat MAS

A GAS programme is operational for the alpha-S1 casein gene for dairy goats in France (Manfredi, 2003). The gene is associated with protein content and protein yield. In this programme, young bucks are pre-selected within families based on genotype. The programme is run by a cooperative AI centre (Capri-IA) and, although started up with government funding, it is now almost running on a fully commercial basis.

MAS in developing countries

Most breeding programmes in developing countries, if existing at all, are small-scale with modest objectives. Usually, the challenge is to foster the flow of information (measurement and evaluation) as well as the flow of genes (dissemination of improved stock). These processes are often inhibited by infrastructural, logistical and socio-

economic factors. Clearly, gene marker technology will not be the first priority in many of these programmes. However, where gene tests exist for clearly defined characters with substantial economic benefit, gene markers and MAS could be very beneficial. Introgression of disease resistance genes into productive breeds could be of great value, but few of these examples exist in sheep and goats.

A good example of a clear gene effect successfully implemented in a MAI programme is found in India (Nimbkar *et al.*, 2005). The Booroola gene is being introgressed here from the small Garole breed into the local Deccani breed that is suitable for meat production but has a limited reproductive performance. The Booroola gene has tremendous economic effects in this production system, raising the weaning rate by nearly 50 percent. The breeding programme is undertaken by a research institute, but there are clear strategies and activities to ensure that the improved stock finds its way to shepherd flocks. Evaluation of the results in these shepherd flocks is an explicit part of the project, and initial results look very promising. Therefore, MAS and MAI should not be ruled out for breeding programmes in developing countries, but should be assessed based on the merit of each case. However, implementation of gene marker technology will only work within the framework of a sound existing breeding programme, ensuring the prerequisite that genetic information is valued and that the gene marker accounts for substantial economic merit.

CONCLUSION

Sheep and goat breeding programmes exist in low- to medium-input agricultural systems where there are many independent breeding units and where trait recording

and genetic evaluation are provided by external service agents. This situation is different from that in poultry and pigs and to some extent dairy, and more similar to that in beef cattle, in the sense that the business units that invest in genetic information are not the same as those providing genetic evaluation, and EBVs are available in the public domain. Also, genotypic information is an explicit part of the marketing of genetic material. The result is that genotypic information is more likely to be used outside the usual EBV system, with the chance of being overvalued once the investment is made. There is a place for MAS and MAI based on genetic tests for clearly demonstrated phenotypic effects with economic benefit, for example for disease, fecundity and meat quality.

The number of detected and confirmed QTL is low for sheep and goats and gene mapping is less advanced than in other livestock species. There is significant investment and progress being made in marker development and gene discovery, but it will take some years before large amounts of genetic information become available at little cost, e.g. in the form of SNP chips. Until then, genotypic information will provide additional selection criteria, making optimal selection a greater challenge.

Ultimately, the additional value of gene markers will be greatest in breeding programmes that already use intensive pedigree and performance recording, and it will help to shift selection pressure towards traits that are hard to improve based on phenotypic (BLUP) selection (i.e. traits such

as fertility, disease resistance and carcass quality). It is not essential that genetic tests are based on functional mutations, as gene markers can have predictive value due to being in linkage disequilibrium with functional genes. In breeding programmes without extensive recording, it is more important to rely on direct markers, but this will only be valuable in practice if genes have very large economic effects. The same holds for genetic tests for distinct Mendelian traits, but the overall value of these traits in breeding programmes is limited. In less-developed breeding programmes, investments in pedigree and performance recording will most likely be more profitable than investments in gene technology.

Application of MAS or MAI in many sheep and goat breeding programmes in developing countries is not a priority, but opportunities exist, conditional on having a clearly visible phenotypic effect and a programme based on well-defined objectives and performance based selection.

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