MEAT SHEEP BREEDING – WHERE WE ARE AT AND FUTURE CHALLENGES

N. M. Fogarty

NSW Department of Primary Industries, Orange Agricultural Institute, Orange, NSW 2800

SUMMARY

Developments in meat sheep breeding in Australia over the last 40 years are reviewed. This includes the evolution of LAMBPLAN and its implementation in the industry, development of breeding objectives and estimation of genetic parameters. The development of indexes and the importance of major genes for both meat and maternal traits are discussed as well as strategies for combined improvement of wool and meat in Merino enterprises. Opportunities and challenges for breeding in the future are considered.

INDUSTRY BACKGROUND

Performance recording programs to assist meat sheep breeders were first developed in the late 1960s by the NSW, Victorian and SA Departments of Agriculture and the University of NSW (Pattie 1973). Their development was advocated as a means of increasing the rate of genetic improvement in economically important traits, by the Animal Production Committee Expert Panel (APC 1970) and by several workshops over the next decade, although they failed to attract widespread usage by breeders. However in the late 1970s Dorset breeders showed renewed interest in production testing following industry developments that included: demonstration of within flock variation in measured growth and fatness in Dorset production competitions (Fogarty and Harris 1975; Clements and Fogarty 1976); increased focus on carcase weight and fat in carcase classification and lamb marketing (Moxham and Brownlie 1976); strong consumer preference for leaner cuts (Thatcher 1982); use of fleece measurement in Merino breeding (McGuirk 1978); development of technology to accurately measure fat depth in live animals (Thompson *et al.* 1977; Clements *et al.* 1981); and the success of Sheeplan in New Zealand (Clarke 1979). The NSW Meat Sheep Testing Service (MSTS) was implemented in 1980 with widespread support from Dorset and other terminal sire stud breeders in NSW (Harris 1985) and it expanded to testing over 17,000 sheep from 120 studs annually (Fogarty *et al.* 1987). The program of R&D and advisory support was run by the NSW Department of Agriculture from Cowra with financial support from the Australian Meat and Livestock Research and Development Corporation (now Meat and Livestock Australia, MLA). The objective of the project was to “evaluate the development of a viable facility enabling meatsheep stud breeders to objectively test rams for genetic differences in growth rate and fat depth”. The project developed practical procedures for measuring fat depth using real-time ultrasound technology, accumulated a large database and provided a model for the development of LAMBPLAN, the national genetic evaluation program that was launched in 1989 (Banks 1990). A procedure was also developed for measuring eye muscle depth using real-time ultrasound in live animals (Gilmour *et al.* 1994) and included in LAMBPLAN (Fogarty *et al.* 1992a).

Genetic improvement of growth and leanness of terminal sire rams using LAMBPLAN was a key element in the Elite Lamb R&D Program (Thatcher 1992) and Strategic Plan adopted by the industry in the 1990s to produce large lean lambs. A national program of central progeny testing of terminal sires in the early 1990s (Banks *et al.* 1995) contributed to the adoption of LAMBPLAN (Banks 1994). Studies also demonstrated that rams with a range of LAMBPLAN estimated breeding values (EBVs) produced lambs with predictable performance (Hall *et al.* 1995; Hall *et al.* 2002) and there was considerably more variation between individual sires than between terminal sire breeds for growth (Fogarty *et al.* 2000a) and carcase (Fogarty *et al.* 2000b) traits. Buyers also began to pay a premium at auctions for flock rams with high EBVs (Ferguson and Fogarty 1997).

More sophisticated software was developed using an animal model and BLUP procedures to estimate EBVs across flocks and years (Gilmour and Banks 1992). For the first time in Australia, breeders were able to compare the genetic merit of sheep in different flocks, which led to a greater uptake of LAMBPLAN, with over 50% of terminal sires in the industry being tested by 1994 (Banks 1994). The larger data sets required new software (Brown *et al.* 2000) and a joint program of MLA and Australian Wool Innovation Ltd (AWI) incorporated Merinos into the national sheep genetic evaluation system (Brown *et al.* 2006, 2007). The Sheep Genetics databases include records on over 1.3m terminal sire, 0.3m maternal and 1.1m Merino animals (Brown *et al.* 2007). There has been substantial improvement in all breeds between 1990 and 2005, with terminal sires increasing by $17/ewe (2.9 s.d.) and an increased genetic trend since 2000 (Swan *et al.* 2009).

While uptake of the new genetic technology was high in the terminal sire sector of the industry in the 1990s, the maternal breeding sector was lagging, despite having EBVs and genetic information available for the economically important reproduction and wool traits (Fogarty *et al.* 1992a). Productivity of the crossbred ewe flock has a major impact on the profitability of lamb enterprises and the task was to achieve greater genetic improvement among the commercial flocks of crossbred ewes. To address this issue the Maternal Sire Central Progeny Test (MCPT) project commenced in 1997 (Fogarty *et al.* 1999), to evaluate and demonstrate the variation in first and second cross progeny performance of maternal and dual purpose (wool and meat) sires and the scope for genetic improvement in the sector. The MCPT demonstrated that there was a range of over $40 gross margin/ewe/year between first cross ewe sire progeny groups (Fogarty *et al.* 2005).

Recently considerable investment has been made in SheepGenomics to "find useful genes and put them to work" (Oddy *et al.* 2007). A resource population has been developed to find quantitative trait loci (QTL) and a greater understanding of functional genomics. The Cooperative Research Centre (CRC) for Sheep Industry Innovation has also developed the Information Nucleus (IN), which progeny tests key young industry sires for an extensive range of traits in widely differing environments (Fogarty *et al.* 2007a). This allows breeders and commercial producers to exploit new technology and genomic information to achieve more rapid genetic improvement.

BREEDING OBJECTIVES AND STATISTICAL DEVELOPMENTS

Studies showed the importance of including liveweight (Stafford and Walkley 1979) and carcase fat (Atkins 1987; Clarke *et al.* 1991) in the breeding objective for meatsheep. LAMBPLAN initially provided within-flock EBVs for weight and fat depth based on live animal measurements and information from correlated traits and relatives (Banks 1990). Eye muscle depth was subsequently included (Fogarty *et al.* 1992a). The breeding objectives for maternal meatsheep breeds include reproduction and wool, in addition to weight, fat and muscle (Fogarty 1987). In 1992 there was a major enhancement of the statistical procedures used for estimation of genetic merit in LAMBPLAN with the development of animal model BLUP software, BVEST (Gilmour and Banks 1992). BVEST was designed to perform on-farm breeding value estimation for individual cohorts of animals and off-farm across flock and across year estimation, using performance information from relatives and all available pedigree records. Muscle depth and maternal traits were also included in this enhancement.

New software (OVIS) was developed in the late 1990s to handle the large data sets, include more traits and breeds and incorporate new features such as an expanded model with maternal and permanent environmental components and genetic grouping (Brown *et al.* 2000). Subsequently, significant development was required to incorporate Merinos to deliver a single national across-flock genetic evaluation system to the Australian sheep industry. These innovations included the amalgamation of databases, data transformations, refinement of analysis models, genetic grouping methodology, updated genetic parameters, multiple trait across-flock linkage assessments, index development, use of a common technical language and changes to reporting (Brown e*t al.* 2007).

GENETIC PARAMETERS

The MSTS dataset was used to validate adjustment procedures (Fogarty and Luff 1985) and provided the first genetic parameter estimates for weight and fat depth in Australian Poll Dorset sheep (Atkins *et al*. 1991) and several other meat and dual purpose breeds (Brash *et al.* 1992). A major program was undertaken to estimate genetic parameters for a range of other economically important traits using research and stud data sets from Border Leicester (Brash *et al.* 1994a), Corriedale (Brash *et al.* 1994b), Coopworth (Brash *et al.* 1994c) and Hyfer (Fogarty *et al.* 1994) breeds, so that breed-specific parameters could be used for calculating EBVs (Fogarty *et al.* 1992a). Genetic parameters in Australian Dorset sheep were also estimated for reproduction traits (Brash *et al.* 1994d), eye muscle depth in live animals (Gilmour *et al.* 1994) and an extensive range of carcase and meat quality traits (Kenney *et al.* 1995). These estimates together with a review of the world literature provided the basis for the early genetic parameter matrix used in LAMBPLAN (Fogarty 1995).

Safari and Fogarty (2003) tabulated 164 reports of sheep genetic parameters for a range of traits published in the world literature over the previous decade. These reports provided weighted means of the parameter estimates for the traits in a review (Safari *et al.* 2005). The review showed there were numerous estimates of heritability, which were reasonably consistent, for wool, growth and, to a lesser extent, reproduction traits, although there were few estimates for carcase and meat traits. The review also showed that while there were several estimates of genetic correlations among the various wool and growth traits, there were very few, if any, among the other trait groups or between the various trait groups. To address this dearth of genetic correlation parameters the Australian Sheep Industry CRC and owners of several research data sets supported a combined analysis. Seven Merino research data sets were combined (Safari *et al.* 2007a) and heritabilities (Safari *et al.* 2007b) and genetic correlations (Safari *et al.* 2007c) among and between a range of wool, growth and reproduction traits were estimated with high accuracy. In addition, genetic parameters were estimated for carcase and meat quality traits (Fogarty *et al.* 2003b; Greeff *et al.* 2008), as well as genetic correlations between carcase and meat quality traits and growth and wool traits (Greeff *et al.* 2008) and ewe reproduction traits (Safari *et al.* 2008). Additional parameter estimates have recently been published for fine wool Merinos (Swan *et al.* 2008) and Merino flocks recorded in the Sheep Genetics database (Huisman *et al.* 2008; Huisman and Brown 2008, 2009a, 2009b). The MCPT data set was also used to estimate genetic parameters for lamb growth, carcase and meat quality, wool production, worm egg count (Ingham *et al.* 2007), feed intake (Fogarty *et al.* 2006a), reproduction (Afolayan *et al.* 2008b), insulin-like growth factor-1 (IGF-1) (Afolayan and Fogarty 2008) and milk production (Afolayan *et al.* 2009c) in first cross animals, together with the genetic correlations between ewe reproduction traits and early growth and wool production (Afolayan *et al.* 2009a), growth and carcase performance of their progeny (Afolayan *et al.* 2008a) and between milk and other production traits of the ewes (Afolayan *et al.* 2009b).

MEAT TRAITS

Indexes. LAMBPLAN initially offered a range of simple indexes to assist in selection of animals for a combination of increased growth rate (post weaning weight) and decreased subcutaneous fat (Banks 1990; Fogarty *et al.* 1992a). The option of eye muscle depth as an additional trait in these indexes for terminal sires was subsequently included (Banks 1994). A wider range of indexes is now available, with two specifically designed dollar indexes for breeding objectives to meet the domestic (20-22 kg carcase weight) and export (24+ kg carcase weight) markets (Brown *et al.* 2000, 2007). Recently the LAMB 2020 dollar index was launched by Sheep Genetics, which as well as combining weaning weight, post weaning weight, leanness and muscle depth, includes a negative emphasis on birth weight and increased resistance to worms (Ball 2008).

Major genes. In the early 1990s a major gene (callipyge) was shown to increase hindquarter muscling and meat toughness in Dorset sheep in the USA (Koohmaraie *et al.* 1995). Sires from Australian Dorset flocks were also shown to carry a similar gene (Carwell), although its effects on loin muscling and tenderness were much smaller than callipyge (Hopkins and Fogarty 1998b). The Carwell allele increases eye muscle weight by 8% and area by 10% (Nicoll *et al.* 1998). The gene is maternally imprinted and has been mapped to a region near callipyge and a marker test is available (Dodds 2007). Another gene has also been found which increases leg muscling and reduces fat in Texel sheep and a marker test is available. It appears to be additive and may be associated with myostatin (Dodds 2007).

MATERNAL TRAITS

Indexes. LAMBPLAN was enhanced in the early 1990s to include reproduction and wool traits, as well as growth, fat and muscle, for maternal and dual-purpose breeds (Fogarty *et al.* 1992a). Reproduction is more important in maternal than Merino breeding objectives and was sensitive to prices and varied in importance for different dual purpose breeds (Fogarty and Gilmour 1993). It is also important to take into account the feed requirements of the maternal flock as well as the lamb progeny in overall enterprise profitability (Fogarty *et al.* 2003a). Dollar indexes are available in LAMBPLAN which are customised for each of the maternal breed groups (Brown *et al.* 2007). Selection on litter size or ovulation rate to increase reproduction was advocated in the 1970s and 1980s, however there is considerable genetic variance for all components of reproduction (Safari *et al.* 2005) and use of a selection index of overall ewe productivity or litter weight weaned may result in a more balanced biological outcome (Snowder and Fogarty 2009). There are several reports demonstrating realised response to selection for litter weight weaned (Fogarty 1994; Ercanbrack and Knight 1998; Cloete *et al.* 2004).

Major genes. A series of experiments in Australia and New Zealand in the early 1980s confirmed the high prolificacy of the Booroola Merino was due to the segregation of a major gene (FecB) (Davis *et al.* 1982; Piper *et al.* 1985), with a molecular test now available (Davis 2004). A recent review of 40 studies in a range of genetic comparisons, environments and production systems (Fogarty 2009) showed the effect of heterozygous (B+) versus non-carrier (++) ewes was +1.1 to +2.0 for ovulation rate (with BB generally being additive) and +0.5 to +1.3 for litter size (with little additional effect for BB). Poor lamb survival and growth, due largely to higher litter size, further reduced the effect for lambs weaned and weight of lamb weaned. Poor lamb survival and associated low birth weight and growth have been major barriers to industry uptake in Australia despite FecB being introgressed into research and commercial flocks. Several other genes that have major effects on ovulation rate have also been reported in overseas breeds (Davis 2004).

COMBINING MEAT AND WOOL

Meat and wool have long been regarded as separate industries, with prime lamb production based on crossbred progeny of terminal sires and first cross dams and apparel wool being the preserve of the Merino (Pattie 1973). There are different breeding objectives for terminal sires (Atkins 1987), prime lamb dams (Fogarty 1987) and Merinos (Walkley 1987), although the Merino has always contributed a majority of genes to the national lamb slaughter through second cross, first cross and straightbred Merino lambs (Fogarty *et al.* 2000a). While Merino and first cross lambs have lower growth rates than second cross lambs (Fogarty *et al.* 2000a; Hopkins *et al.* 2007), there is little difference in their carcase and meat quality performance when grown under the same conditions and compared at the same carcase weights (Hopkins and Fogarty 1998a, 1998b; Fogarty *et al.* 2000b; Ponnampalam *et al.* 2007).

The increasing demand and economic value of lamb and the relative decline in value of wool has meant that more Merino ewes are being mated to terminal sires and many Merino breeders wish to include meat traits in more complex breeding objectives, although development of a dual-purpose sheep is not recommended (van der Werf 2006). There are no major genetic antagonisms between meat and wool traits and improvement can be achieved in both using an appropriate selection index (Fogarty *et al.* 2006b). The genetic parameters (heritabilities, variances and genetic correlations) estimated in Merino and crossbred sheep in the reports noted above now provide comprehensive information for developing more complex breeding objectives and selection criteria for combining meat and wool traits.

OPPORTUNITIES AND CHALLENGES

Meat quality. A key element in the revolution that has occurred in the lamb industry over the last two decades has been improvement in products and quality. Subcutaneous fat has been reduced and muscle size increased while maintaining a high level of eating quality. However selection for muscling can result in structural and biochemical changes to muscle, with less aerobic muscle, less intramuscular fat and sometimes a reduction in tenderness (Pethick *et al.* 2006). It is critical to develop a better understanding of these potentially detrimental effects on meat quality (part of the Meat Program in the Sheep CRC) and ensure appropriate breeding programs are implemented by industry. There will also be increasing consumer interest in meat products that meet specific health standards or confer particular human health benefits (Bermingham *et al.* 2008). An example may be increasing the level of long-chain omega-3 fatty acids in lamb (Pethick *et al.* 2006).

Fitness and reproduction. Net reproduction is low in most Australian and particularly Merino flocks. Improving post natal and embryo survival is critical as ovulation rate is generally not limiting. Poor lamb survival is an animal welfare issue for the industry as well as one of reduced productivity. There is some evidence of genetic variance and heterosis for embryo survival (see Fogarty 2009), although further research needs to be undertaken. While most reports have shown little genetic variance for lamb survival, there is more variation for ewe rearing ability or lamb survival as a trait of the ewe (Safari *et al.* 2005). Recent analysis of a large Merino data set has shown similar results with repeated records of ewe rearing ability, especially for survival to 7 days, being able to increase selection accuracy and improve current generation performance (S Hatcher pers. comm.). There is also genetic variance for adult longevity (Hatcher *et al.* 2009).

Other opportunities for improving reproductive efficiency in the lamb industry include mating ewes for the first time at an earlier age and accelerated lambing systems. Crossbred ewes can be successfully joined in the autumn to lamb in their first year. Puberty and lambing performance in ewe lambs is influenced by both genetic and environmental factors and ewes that rear lambs in their first year rear more lambs in subsequent years (Fogarty *et al.* 2007b). Accelerated lambing systems can increase annual lamb production of ewes (Fogarty *et al.* 1992b) and improvements can be made by selection (Fogarty 1994).

Whole genome selection. Recent advances in sequencing the sheep genome has opened up the opportunity to exploit whole genome selection (Meuwissen *et al.* 2001). Genomic (G) EBVs can be calculated from the information on thousands of single nucleotide polymorphisms (SNP) that will be available in the near future (Oddy *et al.* 2007). In dairy cattle GEBVs have been shown to be highly reliable and are being used to improve the rate of genetic gain (Hayes *et al.* 2009). The task in sheep is to quantify the effects of useful SNP and to validate these in wider industry sheep populations that have relevant phenotypic data. The SheepGenomics (Oddy *et al.* 2007) and CRC Information Nucleus (Fogarty *et al.* 2007a) are important resource flocks in this quest.

Combining quantitative and genomic information. There are a large number of gene markers (van der Werf *et al.* 2007) and DNA tests available (Dodds *et al.* 2007) for disease and production traits in sheep. Strategies need to be developed to effectively combine the genomic and quantitative information. Davis *et al.* (2006) highlighted some of the problems such as a high merit ram for multigenic traits not being indicative of progeny merit in the presence of a segregating major gene. However, the imminent availability of genotype data for a large number of SNP may make the analysis of the data more straight forward (van der Werf *et al.* 2007).

CONCLUSIONS

Genetic improvement, especially in growth, leanness and muscling, has been a key element in the dramatic increase in productivity and profitability of the meat sheep industry over recent decades. These changes have occurred through development of LAMBPLAN, which has been made possible by the ongoing R&D support, and its widespread adoption by industry.

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