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administrative procedures but does allow for significantly more flexibility in interactions with stakeholders and variation of work programs.

The Coretech Subprogram has been invaluable in bringing together the four industry Subprograms (Wool, Muscle, Parasites and Reproduction) with common tools, resources and services.

DNA markers are likely to be the first products from the program that are made available to industry for enhancing breeding programs. Mechanisms have already been put in place to ensure integration with genetic information in the form of SGA's ASBVs.

The biological basis of variation in sheep's fleece cover

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ABSTRACT

Efficient sheep farming of the future will demand reduced labour costs, ease of shearing, and minimised susceptibility to flystrike, while modern markets simultaneously demand reduced chemical use and high standards of animal welfare. Sheep with a reduced area of the body covered with fleece may provide a practical solution to these conflicting requirements. Research has shown that it is possible to select sheep for bare faces, legs, belly and breech, and that at least some of these traits behave as though they are controlled by recessive genes, but that some only become evident later in life. Patterns of fleece distribution define major skin domains in the sheep that are evident in other mammals. We hypothesise that discrete skin domains arise because fibroblasts that induce wool follicle development originate from different embryonic tissues and carry with them differing developmental programmes for each follicle type. Identifying genes underlying variation in fleece distribution would allow desirable distributions to be established in sheep of diverse genetic backgrounds. Markers for distribution traits would enable us to introgress appropriate genes into flocks that do not carry them, and to determine early in life which animals might express the traits as adults.

Keywords: fleece distribution; regional specification; bare breech; bare belly; wool quality.

INDUSTRY NEED FOR ALTERED FLEECE COVER

The profitability of sheep farming is continually being eroded as input costs rise, while returns for wool decline. In the past, high wool prices led to selection for maximum production, resulting in long wool cover on the head, belly and breech in traditional dual purpose sheep breeds (Figure 1a). The associated husbandry requirements, including crutching, dagging and docking, were justified by the high value of the wool. More recently, in addition to falling prices, dramatic increases in shearing costs have occurred (Rennie, 2006). Two major reasons are: firstly, the Accident Compensation Commission is passing on escalating costs due to shearers injuries (ACC, 2003), and secondly, labour costs are driven up as shearing contractors attempt to attract and retain skilled shearers for a physically demanding job. An optimised fleece distribution would reduce these

costs by improving the ease and efficiency of the shearing process. There would also be no cut teats on ewes with a bare belly, and no cuts on the pizzle or scrotum of rams which has advantages from both production and animal welfare perspectives.

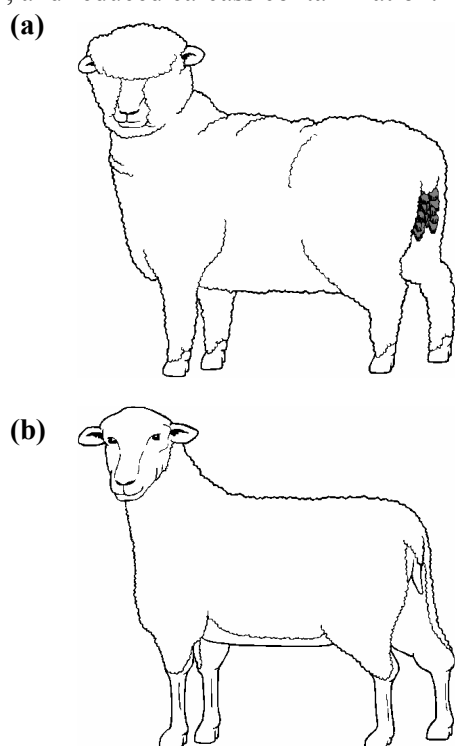
Variations within a harvested fleece also undermine the value of the wool (McDermott *et al.*, 2006). Attributes of the fleece that vary between body regions include staple length, staple strength, fibre diameter and follicle density (Sumner & Craven, 2000). In Romneys, as an example of a typical "woolly" sheep, within-sheep variation in wool characteristics is three-fold greater than that between-sheep (Sumner & Revfeim, 1973).

Long belly wool also significantly increases the incidence of microbiological contamination of sheep carcasses during meat processing. Recent high lamb prices relative to low wool prices provide additional impetus to addressing wooliness of the belly. Furthermore, public awareness of animal welfare has increased, and practices such as

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mulesing and tail docking are becoming ethically unacceptable. Animal activist groups have specifically targeted the use of mulesing for flystrike prevention, forcing Australian wool producers to plan to phase out the practice by 2010. Thus the sheep farm of the future must have animals with valuable, uniform, easy-to-harvest fleeces without the problematic belly and breech wool that has a propensity to become stained, daggy and fly blown.

FIGURE 1: Wool cover patterns. (a): Fleece distribution in Romney-cross dual purpose breeds. (b): Idealised distribution for efficient management, ease of harvesting, reduced flystrike risk, and reduced carcass contamination.



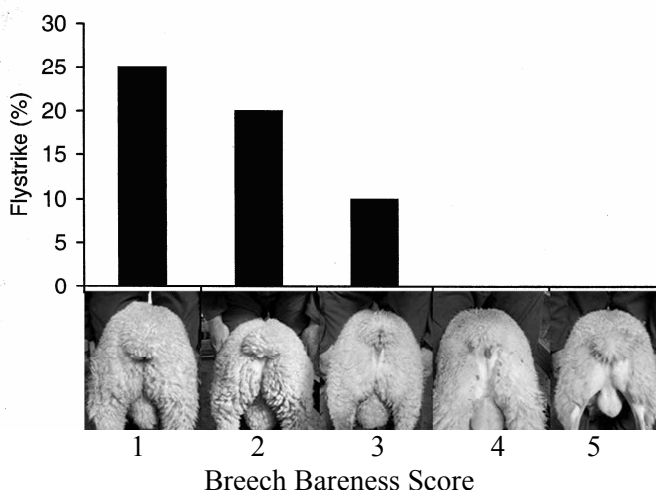
WOOL PRODUCING SHEEP OF THE FUTURE

Scobie *et al.* (1997; 1999a) provided a blueprint for a morphologically new sheep like that in Figure 1b. Such a fleece cover pattern could simultaneously reduce costs and make sheep products more attractive to consumers who are becoming conscious of animal welfare and/or chemical use (Scobie, 2000). By far the most exciting outcome of a sheep with reduced wool cover around the breech is a reduction in flystrike (Scobie *et al.*, 2002). This is associated with a reduction in faecal staining of wool as a consequence of increasing bare area, which has the added advantage of improving dye stability that is a problem in products made from wool contaminated with faeces. There is a phenotypic correlation

(Scobie *et al.*, unpublished data) between bare area and dag score (-0.15 ± 0.03), where 0 = no dags and 5 = a large amount of dags. Since increasing dag score is also undesirable for slaughter hygiene, there are further advantages for meat production.

Scobie *et al.* (1999a) showed that sheep like that depicted in Figure 1b required half the time to shear with only a 20% reduction in fleeceweight. This early research used sheep with a conventional fleece cover like that in Figure 1a, which were trimmed to resemble Figure 1b. An experimental selection flock has since made substantial gains in producing sheep with a restricted fleece cover. Most of the wool that has been removed by selection is lower value oddments which often require removal at other occasions throughout the farming calendar. For example, dagging, crutching, pre-lamb crutching and pre-slaughter preparation all involve removal of parts of the fleece.

FIGURE 2: Increasing bareness of the breech from a score of 1 (woolly breech, on left) to 5 (bare breech, on right) reduces the incidence of flystrike.



To compare the production of sheep like those in Figure 1, ewes from the experimental selection flock were run with Romney ewes from commercial sources. These were both mated to rams from the selection flock that exhibited a bare belly. Belly bareness scores were recorded from 1, which was exceptionally woolly to a score of "5" (Figure 2) which is "perfect" for the diagram in Figure 1b. Selection flock ewes were allocated to rams at random, within belly bareness score groupings, while the Romney ewes were allocated at random within source because they showed no variation in belly bareness with all animals exhibiting a belly bareness score of "1".

Ewe lambs resulting from this mating were run together, shorn as lambs in February and shorn again as hoggets in September. Immediately prior

FIGURE 3: “Black and tan” colour phenotype on the left and bare belly on the right showing regional specification of pigmentation and fibre type. Note the clear boundaries between belly and flank regions. Photo of “black and tan” lamb courtesy Roland Sumner.



to shearing they were scored for belly bareness. The time taken to shear each animal was recorded according to the method of Scobie *et al.* (1999a). The total amount of wool produced and skirted fleeceweights were recorded (Table 1). There was also variation between sire groups, from 1.2 to 1.9 kg of fleece from these ewe hoggets. The selection flock x Romney animals required a similar time to shear as animals from the selection line with an equivalent amount of wool cover, but increasing belly bareness score clearly reduced the time taken to shear. The selection flock x Romney animals produced much more total wool, but this difference was reduced following skirting. The fleeceweight of the hoggets in the selection line varied from 0.8 to 2.8 kg which provides enormous scope to increase fleeceweight by selection. A key point to note is that most animals had woolly bellies and none had a belly bareness score of “5” at 12 months of age. Ideally, sheep in the selection flock would attain a belly bareness score of “5” as early as possible and maintain it throughout life.

Lambing outdoors is the norm in New Zealand, and lamb survival during inclement weather is never far from producers' minds. However, the fear that lambs with bare heads, legs and bellies will die from hypothermia is allayed because these animals are born with a complete coat which in later life changes to wool over the back and around the neck, while hair develops on the belly, breech, head and legs. For example, selection line females ($n = 34$) had mean belly

bareness scores of 2.4, 2.7, 4.5, and 4.7 at weaning, hogget shearing, 18 months and 28 months of age respectively. There was clearly an improvement in mean belly bareness with age. These changes with age complicate selection for which it would be advantageous to be able to predict adult belly bareness.

TABLE 1: Belly bareness score (1 = woolly belly, 5 = bare belly) of ewe hoggets from an experimental selection flock, and ewe hoggets created by mating the sires used in the selection flock with Romneys. The number of ewe hoggets, average time to shear in seconds (Time (secs)), average total wool harvested (Total wool (kg)) and average skirted fleece weight (Skirted fleece (kg)) are shown for each belly bareness score grouping.

Characteristic	Selection flock				Selection flock x Romney	
	1	2	3	4	1	2
Belly bareness	1	2	3	4	1	2
No. of sheep	4	73	30	9	29	29
Time (secs)	104	92	81	71	104	98
Total wool (kg)	2.2	1.7	1.8	1.6	2.7	2.5
Skirted fleece (kg)	1.8	1.4	1.6	1.5	2.2	2.0

A sheep that has a woolly belly in winter and a bare belly in spring is equally possible given the variation observed in the selection flock. Ram lambs that were the siblings of the ewe hoggets in Table 1 were scored for belly bareness at weaning in January 2004 and again in April 2004. Woollier ram lambs were observed at both ages for the

selection flock x Romney ram lambs ($n = 66$, scores of 1.0 and 1.7) compared with the selection flock ram lambs ($n = 115$, scores of 2.3 and 2.5). Overall, 79 animals exhibited an increase in belly bareness score while most remained unchanged ($n = 95$) and only 7 exhibited a decrease. Of these seven lambs, two had begun growing wool again after shedding fleece from the main body region, suggesting changes with season in at least some of the males in this flock. We also believe there is a seasonal fluctuation in belly bareness in some adults in the experimental flock, but we have insufficient data to characterise these changes at this time. In contrast, the adult Romney ewes universally scored belly bareness of 1 at mating and again in December.

Thus, there is a need to understand and improve variation within and between regions and temporal variation within the fleece. Sheep are currently being bred to exploit the heritable, naturally occurring variations in fleece distribution between breeds and within commercial flocks. These phenotypes may represent the combined effect of multiple genes, some of which show different topographic effects. A complementary and ultimately more powerful approach is to determine the developmental and molecular mechanisms that control fleece distribution patterns. This would then allow manipulation of key genes in elite stock, perhaps via a marker assisted selection strategy.

SPECIFICATION OF WOOL-GROWING SKIN REGIONS

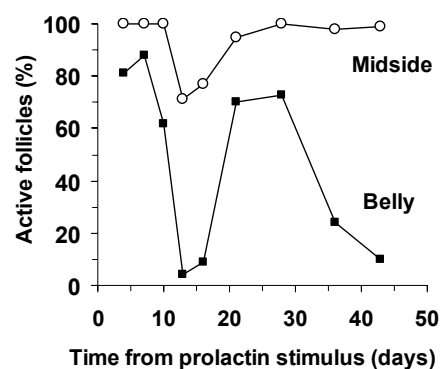
How do regional differences in wool cover come about? The patterns of fleece distribution in sheep correspond to features of pelage and pigmentation seen more generally in other mammals (Candille *et al.*, 2004). In particular, there is a boundary between dorsal and ventral skin domains that is established in the developing embryo. Clear differences between the pelage on the belly and flank of sheep are shown in Figure 3. The biological basis of fleece distribution in sheep is thus part of a larger question of regional specification during early development of the skin.

We propose that differences between dorsal and ventral skin arise because the inductive dermal cells that ultimately determine fibre type originate from different embryonic tissues. This hypothesis is derived from recent advances in knowledge of skin development and the origins of regional specificity, as outlined in the following three arguments.

First, differences in fibre type result from differences in wool follicle behaviour. Long fibres

on the main fleece growing region result when follicles remain in the growth phase (anagen) for prolonged periods, while short fibres on the limbs, breech or belly are grown during a short anagen interspersed with long periods of follicle quiescence (telogen). We have illustrated regional differences in cyclic growth by synchronising wool follicles in Wiltshire sheep with altered levels of circulating prolactin (Figure 4). Wool follicles at the midside shut down briefly then resumed growth to produce the distinctive shed fleece of the Wiltshire. The interruption of growth on the belly was followed by a synchronised anagen lasting only 3-4 weeks, producing correspondingly short fibres (A.J. Craven, unpublished data).

FIGURE 4: Cyclic growth of wool follicles accounts for topographic variation in fibre type. New Zealand Wiltshire sheep were treated with bromocriptine to suppress pituitary prolactin secretion. When this suppression was released in mid summer (day 0), synchronised shedding of wool follicles was induced. The percentage of actively growing wool follicles in skin from sheep killed at regular intervals after release was determined by histology. Growth was briefly interrupted at the midside site (○) and then follicles continued growing long wool fibres. In contrast, synchronised growth on the belly (■) exhibited a short cycle, producing short belly fibres typical of the Wiltshire breed.



Second, follicle formation and behaviour is predominantly governed by cells of the dermis. Skin appendages, including wool follicles, develop through reciprocal interactions between the foetal dermis and epidermis (Millar, 2005). The roles of these two layers have been explored in experiments where tissues from different body sites or species were surgically recombined in the embryo (Sengel, 1990; Dhouailly *et al.*, 1998). The results showed that the dermis determines the spacing, size and type of appendage formed. For example, when dermis-forming neural crest tissue is swapped between quail and duck embryos, cranial feathers develop that are more typical of the donor species

than the host (Eames & Schneider, 2005). In mammals, dorsal and facial dermis from mouse foetuses can induce hair follicle formation in epithelia that normally lack hairs altogether, including cornea (Pearton *et al.*, 2005) and amnion (Fliniaux *et al.*, 2004b). A similar role for dermal cells in the formation of wool follicles in sheep has been postulated (Moore *et al.*, 1998).

Third, the dermis of dorsal, ventral and head regions derive from distinct embryonic tissues (Sengel, 1990). Mesenchymal cells migrate from the somitic dermomyotome to form dorsal dermis (Houzelstein *et al.*, 2000; Olivera-Martinez *et al.*, 2004; Ben-Yair & Kalcheim, 2005), from the somatopleural layer of the lateral plates to form ventral and limb dermis (Fliniaux *et al.*, 2004a), and from the neural crest to form head or facial dermis (Osumi-Yamashita *et al.*, 1994). This aspect of skin development has been largely studied in birds, but the available data indicate that mammalian development is similar (Osumi-Yamashita *et al.*, 1994; Houzelstein *et al.*, 2000; Millar, 2005).

Taken together, these considerations suggest that topographic variations in adult fibre type trace back to differences in the origin of dermal cells during development. The pronounced differences in fibre type between dorsal, ventral and facial skin probably arise from differences in the inductive behaviour of dermal tissue in these three domains. At a molecular-genetic level, we hypothesise that regional differences in dermal tissue are associated with the activation of different combinations of developmental regulator genes.

Prominent candidates for skin region specification are homeodomain-containing transcription factors encoded by homeobox genes. The role of Hox genes in patterning of the anterior-posterior axis has been well established (Deschamps & van Nes, 2005) and underlies regional specification in various tissues (Chuong, 2003). Hox and other homeobox genes show regionally varied expression in the skin of chicken and mouse (Dhouailly *et al.*, 1998; Chuong, *et al.*, 1990; Chuong, 2003). Microarray analysis of cultured dermal fibroblasts showed that expression patterns of 51 homeobox genes were reproducibly correlated with body site, in adult and foetal tissues (Chang *et al.*, 2002). Expression patterns of homeodomain-containing transcription factors are also preserved after transplantation to ectopic sites (Nowicki & Burke *et al.*, 2000). Interestingly, many of the signalling pathways and molecules that are implicated in tissue specificity in the embryo, such as fibroblast growth factors (FGFs), bone morphogenetic proteins (BMPs) and Wnts are also used in later patterning events in the skin and other

tissues (Deschamps & van Nes, 2005; Millar, 2005). Several Hox genes mediate induction of feather and hair follicles (Awgulewitsch, 2003; Jiang *et al.*, 2004) and ongoing growth cycles of the mature organs (Rendl *et al.*, 2005). Thus the expression patterns of Hox genes along the anterior-posterior and dorsal-ventral axes, and also within feather buds and hair follicles, has led to the suggestion that a combination of activated Hox genes - a "Hox code" - conveys positional information in skin (Awgulewitsch, 2003).

WHERE TO FROM HERE?

Since the fleece cover project was proposed (Scobie *et al.*, 1997), and reported in the public press shortly thereafter, there has been a steady stream of inquiry from sheep farmers and ram breeders. Selection for wool cover traits amongst the experimental selection flock has shown that a phenotype that is more suited to current commercial requirements can be achieved. Current initiatives involve searching ram breeders' flocks for animals which express these traits, and investigation into ways to integrate these traits into the national flock.

Genomic technologies offer better opportunities to integrate the traits of interest into sheep populations and hasten genetic progress. Molecular markers for fleece cover traits would be valuable, since some phenotypes usually do not develop until around 18 months of age. Such technologies could help identify animals carrying genes that control fleece cover during early life, to reduce generation interval, and also help to identify animals that exhibit marked seasonal changes in fleece cover. Investigations of the biological mechanisms determining wool cover could facilitate the discovery of useful markers. Genes associated with dorso-ventral patterning could be found by comparing global expression profiles of dermal cells isolated from belly and mid-lateral sites by microarray (Yu *et al.*, 2006). Furthermore, by cross-comparison of bare belly and full-fleeced phenotypes, those genes that are specifically regulated in the bare belly may be identified.

A greater understanding of the underlying biology of regional variation in wool cover could open up possibilities for innovation in wool production. The identification of developmental pathways and individual regulatory genes might present new possibilities for specifying regional variation in the fleece, and therefore provide superior livestock for the sheep farm of the future. For example, alternative wool harvesting technologies based on manipulation of the wool follicle cycle are likely to become apparent once

the controlling biochemical pathways are known. These new technologies could be integrated with more direct grower-manufacturer relationships

where specified wool characteristics, reduced within-fleece variability, and efficient and ethical farm practices will add value.

Microarrays as a discovery tool in wool genomics

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ABSTRACT

Wool follicle development and growth is a highly ordered and complex process involving the sequential expression of numerous genes within diverse cell populations. The aim of present studies using microarray analysis is to identify genes and pathways involved in the growth of wool follicles which could be utilised to increase farm productivity and improve the characteristics of Australasian wools. An ovine cDNA array was developed including sequences derived from sheep skin containing wool follicles in different growth stages encompassing many structural and regulatory genes necessary for follicular growth. Initial comparison of stages of wool follicle regression show marked changes in the expression levels of numerous genes including wool keratins. Two parallel research projects in Australia and New Zealand supported by SheepGenomics are currently utilising microarray technology to profile gene expression during key stages of wool follicle development in the foetus and follicular cycling associated with fleece shedding.

Keywords: gene expression; microarrays; wool follicle development; wool follicle growth cycle.

INTRODUCTION

Innovative technologies are required to address issues of harvesting efficiency, fibre characteristics and animal welfare that are becoming critically important to the future of the wool industry. Such new technologies to control fibre growth will depend on advances in our understanding of the underlying genes and gene networks. For example, genes that encode signalling and adhesion molecules controlling wool follicle morphogenesis in the foetus profoundly affect adult fleece weight and fibre diameter. However, it is likely that the same or similar molecular mechanisms also govern organised interruption and reinitiation of post-natal fibre growth, with associated changes in fibre type and length. Discovery of the gene control networks will provide opportunities to accelerate the rate of genetic progress, and to develop bioactives to transform the costly farming operations of shearing, crutching and mulesing.

The pre-natal development of wool follicles progresses in waves across the surface of the foetus (Hardy & Lyne, 1956; Lyne & Brook, 1964). Ultimately, the nature and distribution of

these follicle populations determine crucial aspects of the wool phenotype including fleece cover and variation in fibre attributes within the fleece (Scobie *et al.*, 2006). Interactions of dermal and epithelial cells initially determine the patterning leading to primary wool follicle formation around day 60 of gestation in Merino sheep (Figure 1). This is followed by the development of original secondary follicles around day 85 of gestation. Branching of the original secondary follicles around day 100 generates the derived secondary follicles. The entire follicle complement is established by shortly after birth (Hardy & Lyne, 1956). Subsequently, and almost uniquely among organs of adult animals, hair follicles in the skin are regularly renewed in a process that, to some extent, recapitulates foetal development (Figure 2). This involves highly regulated inter-cellular communication, follicular stem cell activation, cell migration, proliferation and apoptosis (Stenn & Paus, 2001; Botchkarev & Kishimoto, 2003). These co-ordinated processes lead to the renewal of transient amplifying cells in the follicle bulb which divide and terminally differentiate to form the keratinised wool fibre.

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