

Optimising genetic potential for wool production and quality through maternal nutrition

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Abstract. This paper reviews the development of the wool follicle population with a view to the management of breeding ewes so as to optimise the genetic potential of the progeny for wool production and quality throughout their lifetime. It highlights the importance of the pre-weaning environment (i.e. maternal nutrition through pregnancy and lactation) on the initiation and maturation of the secondary follicle population and identifies the last third of pregnancy as the most critical period. The implications of this for the commercial wool producer are discussed in terms of matching the breeding cycle of the ewes to available pasture and provision of supplementary feed. Finally, it introduces a national project 'Lifetime Wool' funded by Australian Wool Innovation which aims to develop profitable ewe management guidelines for wool growers across Australia to adopt in order to optimise the genetic potential of their flock for wool production and quality.

Keywords: genetic potential, follicle development, breeding ewe, nutrition, lifetime wool

Introduction

With the development and increasing use of electronic identification systems for sheep and the continuing progress in the accompanying hardware and software systems to support electronic data capture and use on-farm, the opportunity exists for the sheep industry to move more towards precision wool growing. Using individual animal identification and on-farm fibre measurement to assist with clip preparation and selecting replacement ewes for the breeding flock has been shown to be an effective means of increasing profit in many wool enterprises (Atkins et al. 2004). The authors further concluded that the real benefit of individual animal measurement will come from additional uses of the information such as implementation of specific grazing groups, allocating ewes to particular sires and strategic use of sheep coats. They believed that options such as these would lead to additional economic benefits from an individual animal identification and measurement system (Atkins et al. 2004). One possible additional use of individual animal identification which could play a key role in improving the profitability of a Merino breeding enterprise in particular is through more intensive management of the breeding flock in order to optimise the wool production of the breeding ewe herself as well as that of her progeny.

Genetics play a key role in determining the potential lifetime wool production and wool quality of an individual sheep. However the environment also plays a significant role. Environmental factors can be divided into pre-weaning and post-weaning influences. The nutritional intake of the ewe during pregnancy and lactation is the governing factor of the pre-weaning environment. The ewes' nutrient intake must be sufficient to satisfy her own bodily needs for maintenance and wool growth as well as supply adequate nutrients to her foetus for growth and development until weaning.

Post-weaning influences largely reflect the impact of changing seasonal conditions and hence feed availability on the functioning of the existing follicle population. In times of abundance such as the spring flush of pasture growth a greater amount of nutrients are available to the follicles in the skin resulting in an increase in both wool growth and average fibre diameter. However as the nutrients available to the foetus pre-weaning, during pregnancy and lactation, can have a significant impact on the development the follicle population there is an opportunity through improved management of the breeding ewe flock, to maximise the wool production and wool quality potential of future generations of Merino sheep.

This paper will review the impact of ewe nutrition during pregnancy and lactation on the developing foetus focussing on maximising the genetic potential of her progeny for lifetime wool production and wool quality. We will place this information in context with the current commercial practices of managing the breeding ewe flock and introduce a national project, Lifetime Wool, which seeks to maximise the lifetime wool production and quality of progeny by improved management of the breeding ewe.

Genetic potential – can we maximise it?

Individual animals inherit their complement of genes from their parents, 50% from each. Selection of parents, both rams and ewes that have been identified as superior for the traits of interest is the starting point to determine the genetic potential of the next generation. The process of meiosis during the formation of gametes in both the sire and dam and the fusion of these gametes at conception provides the genetic blueprint for the animal's potential productivity in its lifetime.

In practice the heritability (h^2) or the degree to which variation in a particular trait is under genetic control, of most wool production and quality traits is moderate to high (Safari and Fogarty 2003). None reach the theoretical maximum of 1 which would occur if the genetic potential of an animal was realised. This confirms that the environment does provide a strong mediating influence. And as a result explains why the phenotype of an animal (i.e. how the genes are expressed) is not necessarily the same as the genotype of an animal.

The maximum number of follicles that a lamb will form is determined genetically (Ryder and Stephenson 1968). Estimates of heritability for skin traits are low to moderate., Total follicle density h^2 ranges between 0.18 to 0.46 (Hill et al. 1997); Mortimer 1987; Purvis and Swan 1997),and secondary to primary (S/P) follicle ratio between 0.21 and 0.52 (Mortimer 1987; Purvis and Swan 1997), depending on the strain of Merino studied.

Marston (1955) recognised nearly 50 years ago that it was rare for pastured sheep to reach their genetic potential for wool production. He concluded that it was possible for poor nutrition during pregnancy and lactation to impose a permanent limitation on the subsequent capacity of sheep to produce wool by reducing the number of follicles developed. Lambs whose mothers are being poorly fed, progeny of young ewes and twin lambs develop fewer follicles and this reduces their adult wool-producing capacity (Marston 1955).

The pre-weaning environment is therefore the critical period for realising the genetic potential of an individual sheep. However as the development of the follicle population occurs at clearly defined stages during the pre-weaning period, 'critical' time frames can be identified during which adequate maternal nutrition is vital to ensure maximum development of follicle population and optimisation of genetic potential.

The follicle group - initiation and maturation

The type and arrangement of follicles in the skin of all sheep regardless of breed, is similar. The follicle population typically consists of a basic group of three primary follicles arranged in rows and a variable number of secondary follicles lying on one side of the trio of primaries (Carter 1943; Carter 1955; Ryder and Stephenson 1968) (Figure 1, see Appendix). All primary follicles are associated with a sweat (sudoriferous) gland, an arrector pili muscle and a sebaceous gland while secondary follicles possess a sebaceous gland only (Carter 1955; Ryder and Stephenson 1968).

There are two stages to follicle development; firstly the follicles are initiated in the skin. This is followed by the second phase, maturation, which indicates that the follicles have formed a fibre and are now 'mature'. No gross deviations in the timing of the development of either the primary or secondary follicle populations have been identified between breeds with almost all secondary follicles being initiated prenatally (Fraser and Short 1960). However, considerable variation has been found to exist both between and within breeds in the rate of follicle maturation. Within the Merino breed the follicle population of the Peppin Merino has been deemed mature at about 6 months while South Australian Merino strains can take up to 15 months for their follicle populations to mature and form fibres (Schinckel 1955a).

Primary follicles

Isolated primary follicles begin forming in most skin regions of the foetus between day 50 and day 70 of pregnancy, these are followed by the rapid appearance of their associated lateral primary follicles between day 75 to 85 (Carter 1943; Carter 1955; Fraser and Short 1960; Hutchison and Mellor 1983) (Figure 2, see Appendix). In Merino sheep, all primary follicles produce a keratinized fibre by 108-110 days of pregnancy (Maddocks and Jackson 1988). This indicates the maturity of the primary follicle population is complete prior to birth (Lyne 1961). Any change in primary follicle density after birth is a result of skin expansion (Lyne 1961; Maddocks and Jackson 1988). Corbett (1979) concluded that is was unlikely that maturation of primary follicles could be affected by under-nutrition without also causing the death of the foetus and the dam.

Secondary follicles

From about day 85 to the end of pregnancy follicle initiation is confined to the appearance of secondary follicles between the central and primary follicles (Carter 1955; Fraser and Short 1960, Hutchison and Mellor 1983). There are two types of secondary follicles, originals (So) which develop directly in the skin and derived (Sd) which develop by budding or branching from So follicles (Hardy and Lyne 1956). The So follicles are formed first, with budding of Sd follicles commencing later in pregnancy (Figure 2, see Appendix). Short (1955a) studied a variety of sheep with a wide range in S/P ratio and concluded that almost all, if not all, of the secondary follicles which ultimately produced a fibre were present in the skin of the lamb at birth. While some secondary follicles have been found to be producing a keratinized fibre between 120 to 145 days gestation (Maddocks and Jackson 1988) a significant number of secondary follicles do not mature (i.e. form a fibre) until after birth. Some up to 4 to 6 months post-birth (Fraser 1954; Schinckel 1955a; Short (1955a). (Short 1955a) found that the maximum rate of maturation of secondary follicles occurs 7-21 days after birth.

S/P ratio

In Merino sheep the total number of primary follicles is fairly constant at different ages and between individuals but the total number of secondary follicles varies greatly between individuals and strains (Hardy and Lyne 1956). The ratio of the total number of secondary follicles to primary follicles, or S/P ratio is a measure of the potential number of wool fibres that can appear under favourable conditions (Hardy and Lyne 1956). Differences between breeds and strains within a breed in the density of their follicle and fibre populations are due to variation in the number of secondary follicles both original and derived (Fraser and Short 1960; Hardy and Lyne 1956) and hence differences in the S/P ratio.

The adult S/P ratio of Merino sheep is generally accepted to be about 20:1. However considerable variation exists between Merino strains in S/P ratio (Table 1, see Appendix). A feature of this table is the substantial overlap in the ranges reported for the various strains. This is due to the variation in ages of the sheep sampled in the various studies as Merino strains differ in the age at which follicle maturation is complete (Schinckel 1955a).

S/P ratios range from 2.0 to 4.0 at birth (Fraser 1954), however this is much lower than the adult S/P ratio which suggests that significant maturation of secondary follicles occurs post-birth.

Both Doney and Smith (1964) and Hutchison and Mellor (1983) theorised that the potentially high S/P ratio of the Merino would make it more prone to factors affecting follicle development than breeds with a lower S/P ratio. This theory also suggests that fine and superfine Merinos which tend to have higher S/P ratios than broader strains would also be more susceptible to pre-natal and early post-natal nutritional deficiencies than broader strains.

Time series investigations of the development of skin follicles in Merino sheep, assessed by observing changes in the S/P ratio, have identified the period from 30 days prior to birth to 35 days after birth as the critical period during which that nutritional level is critical to the optimal development of the follicle population (Fraser and Short 1960; Short 1955a).

Maternal effects and the follicle population

The maternal environment can have a large influence on the phenotype of the progeny, especially in sheep production where progeny are reared on their dams. Maternal effects are defined as any contribution, influence or impact on the phenotype of an individual attributable to the phenotype of its dam (Hohenboken 1985). Maternal effects, both pre- and post-natal, are largely related to the level of nutrients made available to the foetus during pregnancy and to the progeny during lactation. The litter size, age of the dam and the nutritional regime experienced by the ewe herself are all contributing factors which can significantly impact on the supply of nutrients to the developing foetus and new-born progeny which have the potential to impact on the follicle population. Generally the litter size effect is greater than that of age of the dam, however the magnitude does vary both within and between production traits of interest (i.e. skin versus fleece traits), with age of the animals and with breed (Hatcher 1995).

Three quite different experimental strategies have been used to quantify the degree of nutritional deprivation required to manipulate the follicle population. The first method involved studying the skin and fleece characteristics of twin born lambs compared to single born lambs (Schinckel 1953) and in some instances also varying the post-natal nutritional level of the twins and singles (Doney and Smith 1964). The second strategy involved maintaining ewes at different planes of nutrition at various stages prior to joining, during pregnancy and lactation and studying the effects on the S/P ratio of lambs born to these ewes (Everitt 1967; Hutchison and Mellor 1983; Kelly et al. 1996; Schinckel and Short 1961; Williams and Henderson 1971) while the third involved varying post-weaning nutrition (Allden 1968; Krausgrill et al. 1997).

Regardless of the experimental method used, these studies have found that prenatal nutritional stress influences only the secondary follicle population. This is in agreement with (Corbett 1979) who concluded that the primary follicle population is unaffected. There is, however, disagreement among the published authors as to whether the pre-natal effects on the secondary follicle population are permanent (Hutchison and Mellor 1983; Kelly et al. 1996; Schinckel and Short 1961; Short 1955a; Everitt 1967) or transitory (Denney 1990; Doney and Smith 1964; Hutchison and Mellor 1983). This disagreement can be the result of three possible causes; namely breed differences, the severity of the nutritional stress and the timing of the nutritional stress.

Breed differences

The expression of maternal effects differs between breeds (Hatcher 1995); (Ryder and Stephenson 1968). In addition breeds differ in both their ultimate S/P ratio and the rate at which the follicles mature. In general, breeds with less 'evolved' fleece types than the Merino have lower S/P ratios and their follicle populations generally mature prior to birth and seem to be less susceptible to the impacts of nutritional stress (Carter and Clarke 1957; Doney and Smith 1964; Ryder and Stephenson 1968).

Severity of nutritional stress

With respect to the severity of the nutritional stress experienced by the ewe, most of the studies involving twin versus single born lambs tended to find smaller differences in S/P ratio and subsequent wool production and quality than those studies which imposed nutritional stress on the ewes during pregnancy and lactation. In addition, the twins versus singles studies generally concluded that the impact of nutritional stress was largely transitory with twin born lambs largely compensating for the differences by hogget age (Schinckel 1953). Other studies investigating different 'maternal handicaps' (i.e. maiden versus adult dams) have also found the effects to be transitory (Lax and Brown 1967) and can be significantly reduced if a high plane of nutrition is provided post-natally (Doney and Smith 1964; Gallagher and Hill 1970; Short 1955a; Schinckel 1955b; Schinckel and Short 1961).

In contrast the work of Everitt (1967), Hutchison and Mellor (1983), Kelly et al. (1996), Schinckel and Short (1961) and Williams and Henderson (1971) all imposed a more severe nutritional regime on the ewes and found the effects on the follicle population and subsequent wool production and quality to be permanent. The severity of the nutritional treatments imposed in some of these studies would be unlikely to occur under commercial conditions without causing the death of the dam and the progeny. As an example the ewes in the low nutritional group reported by Schinckel and Short (1961) were unable to be weighed after day 100 of pregnancy as they were too weak to walk to the weigh crate and a significant number of these ewes had to be assisted at lambing.

In only two studies would the nutritional regime imposed on the ewes be likely to occur under conditions of normal farming practice. In the first, Kelly et al. (1996) used cloned embryos implanted into ewes and fed half the ewes on a submaintenance diet from day 50 of pregnancy so they would lose 7-10 kg maternal bodyweight until lambing. This regime was chosen to mimic conditions commonly found in autumn lambing ewes in WA. Progeny born to the submaintenance ewes had a significantly lower S/P ratio at birth and at both lamb and hogget shearings (0.4 and 1.4 years of age respectively). Interestingly, there was no significant different between the two groups at weaning and there was also variation in the magnitude of the difference between the groups with sampling sites.

In the second, Denney (1990) allocated 25 pregnant ewes to 35 farms in central NSW between day 45 and 62 of pregnancy over two years. All progeny were weaned between 10 to 17 weeks of age and then run together in a single mob until 36 months of age. No significant impact of the preweaning environment was detected in S/P ratio.

Timing of the nutritional stress

Hutchison and Mellor (1983) varied the nutritional intake of ewes by one to two-thirds at various stages of gestation and concluded that the timing of the nutritional deprivation was an important determinant of secondary follicle initiation. When their ewes were severely underfed during the last third of pregnancy (days 112-132) the S/P ratio was not increased by subsequent refeeding. However no such effect was observed when the ewes intake was severely decreased during mid-pregnancy (days 95-116), which indicates that initiation of the secondary follicle population is more susceptible to maternal under-nutrition in the last third of pregnancy. This is not surprising as this period corresponds to the period of maximum secondary follicle initiation (Fraser 1954; Fraser and Short 1960). Hutchison and Mellor (1983) observed that the nutritionally deprived foetuses had distinctly shorter and finer fleeces than the well fed controls and conclude that follicle maturation was also impacted. However as they did not measure any of the progeny after birth it is not know how long these effects persisted.

Follicles and fleece characteristics

Nutritional modification of the follicle population pre-weaning does have an impact on the wool production and wool quality of the progeny. In general, lambs born to underfed ewes tend to grow less clean wool that is broader then lambs born to better-fed dams (Denney et al. 1986; Denney 1990; Everitt 1967; Kelly et al. 1996; Schinckel and Short 1961; Short 1955b), but again the differences observed and their persistence throughout the life of the progeny depended on the severity and timing of the nutritional restriction during pregnancy.

Matching the breeding cycle to feed availability on farm

The timing of breeding operations for most self-replacing wool enterprises is based on optimising the conditions for the lambs birth, growth and development. In accordance with this, most Merino enterprises in Australia work on an autumn joining, leading to a mid- to late-winter lambing, and thereby allowing the spring feed flush to be utilised by growing lambs.

However, by timing their operations in such a way, wool producers may be compromising the future wool production potential of their lambs as the ewe is subject to maximum nutritional stress due to a lack of available green feed and inclement weather during pregnancy.

For the wool growing areas of NSW, there is an average increase (over a range of pasture and grazing crop types) of 286% between the mid-winter and early-spring pasture growth (NSW Agriculture 1996). As a result the nutrition, liveweight and fat score of breeding ewes varies considerably throughout the year due to fluctuations in the quality and quantity of feed available (Ferguson et al. 2004b).

By timing operations to make use of the pasture conditions in spring for lamb growth and ewe lactation, wool producers are inadvertently limiting the pasture nutrition available to the pregnant ewe during the winter months. It is during this period of pregnancy that the extra energy available to the ewe from a higher quality and quantity of pasture could be utilised for secondary follicle development by the foetus..

Pasture growth is limited during the winter months due to cold temperatures. The severity of this limitation is determined by the climatic conditions of the local area where the pasture exists. Localities that endure milder winters have a higher pasture growth rate during this time than those areas that experience very cold winter temperatures. Ewes are often not able to maintain fat score, ensure foetus growth and sustain core temperature during these conditions as the pasture on offer is not adequate for their requirements. Temporary increases in maintenance requirements for sheep can jump 50-70 per cent due to wind, low temperature and rain (Finn 1994). The first attribute to suffer is their body condition or fat cover, as they strip their own fat reserves to maintain their growing foetus.

Implications for commercial wool producers

To overcome this shortfall of feed during pregnancy, producers must either plan to feed supplements to the ewes or carry over sufficient pasture reserves from the previous spring and summer to maintain the ewes in adequate condition during pregnancy. If feed is carried over, producers must ensure that it is of high enough digestibility and height to meet minimum ewe requirements.

Langford, et al. (2004) states that maintaining ewes in a fat score of 3 to 4 from joining to day 75 and then between fat score 3 to 3.5 up until lambing is ideal for foetus growth and maintaining sufficient reserves for lactation while limiting lambing mortality due to over fat.

To meet these fat score targets, producers need to assess both their pastures and their animals live weight and fat score. Pasture needs to be assessed to determine if the amount of dry matter on offer is of sufficient height and quality so as not to limit intake of the pregnant ewe, allowing her to maintain energy requirements. If the pasture is assessed as less than suitable for her and her growing lamb’s requirements, a paddock with suitable pasture or supplementary feeding should be considered. This supplementary feeding to keep ewes above a fat score 3, although expensive, can usually be justified in terms of limiting lamb mortality tender wool (NSW Agriculture 2001).

In the last trimester of pregnancy, the feed requirement for a ewe carrying a single lamb is up to twice the maintenance ration for dry stock while that of a ewe carrying twins is two and half times maintenance ration (Finn 1994). This presents a management problem for sheep producers, especially if they are supplementary feeding, as the requirements of twin and single bearing ewes differ greatly.

One way to better manage the differing nutritional requirements of the single- and twin-bearing ewes is to separate and manage them differently based on pregnancy scanning results. Pregnancy scanning is done at approximately day 100 from joining, dependent upon the operator and the ultrasonic equipment that they use. Ewes can be drafted accordingly to their pregnancy state, and placed on pasture conditions that are suited to their nutritional requirements. This allows the producer to specifically target the two separate mobs of ewes to maintain the ideal fat score levels for the remaining trimester of the pregnancy.

The key is to determine strategically targeted nutritional requirements in a cost effective manner. The aim is to determine how much it will cost to feed the ewe at the critical stages of pregnancy and lactation that will be offset by the increased wool production and quality of her progeny.

Lifetime Wool – optimising wool production and quality

'Lifetime Wool' is a national project funded by Australian Wool Innovation to develop profitable ewe management guidelines for wool growers across Australia (Thompson and Oldham 2004). Optimal allocation of feed resources to breeding ewes is dependent on the clear identification of the critical periods during the reproductive cycle where nutritional manipulation can influence progeny lifetime performance as well as the level of nutrition required to produce these responses (Thompson and Oldham 2004). The first phase of Lifetime Wool involved plot-scale research in both Victoria and WA. Ewes at each site were fed to maintain or lose weight during early- and mid-pregnancy, before grazing different levels of pasture. This type of dose-response experiment will determine the level of ewe nutrition needed at different stages of the reproductive cycle to optimise both wool and meat production per hectare (Thompson and Oldham 2004). Results to date indicate that the wool production and quality (Paganoni et al. 2004c) and reproductive performance (Oldham and Thompson 2004) of the breeding ewe as well as birth weights, survival (Ferguson et al. 2004a), growth rates (Paganoni et al. 2004d) wool production and quality (Ferguson et al. 2004c), body composition (Paganoni et al. 2004b) and worm resistance (Paganoni et al. 2004a) of progeny can all be affected by improved nutrition of the breeding ewe.

The second phase of Lifetime Wool involved paddock-scale research and demonstration where the findings of the plot-scale research are applied to commercial flocks of breeding ewes at 15 sites across southern Australia (Oldham et al. 2004). These 15 sites will also further explore the performance of twins versus single progeny as well as aid in developing the optimal management guidelines. At each of these sites, commercial mobs of 1000 breeding ewes were joined as a single flock. From day 21 of joining 2 random subsets of the original flock are managed to achieve predetermined liveweight and fat score targets based on monthly measurements of ewe liveweight and fat score and the quantity and quality of all feeds on offer (Oldham et al. 2004). The quantity and quality of wool produced by the progeny will be measured on all progeny of each flock for 2.5 years.

In addition the 15 sites will allow estimates of the variation in ewe and progeny response to the environment and genotype to be made. This will add further commercial relevance to the optimum management guidelines for ewe nutrition that will be a key outcome of this project.

Conclusion

Breeding alone and careful selection of superior genetics will not lead to the expression of the full genetic potential of an animal for wool production and quality throughout its lifetime. Minimising adverse environmental conditions, particularly during the last third of pregnancy when secondary follicles are initiated and prior to weaning when these follicle mature is essential to allow progeny of breeding ewes to maximise the expression of their genetic potential. The national Lifetime Wool project will develop guidelines to enable commercial wool producers to strategically manage the nutrition of their breeding ewes in a cost effective and sustainable manner. This is expected to benefits not only the lifetime wool production and quality of the progeny but also their survival, growth and parasite resistance. Additional benefits are also likely to be seen with respect to the wool production and quality, reproductive efficiency and disease resistance of the breeding ewes.

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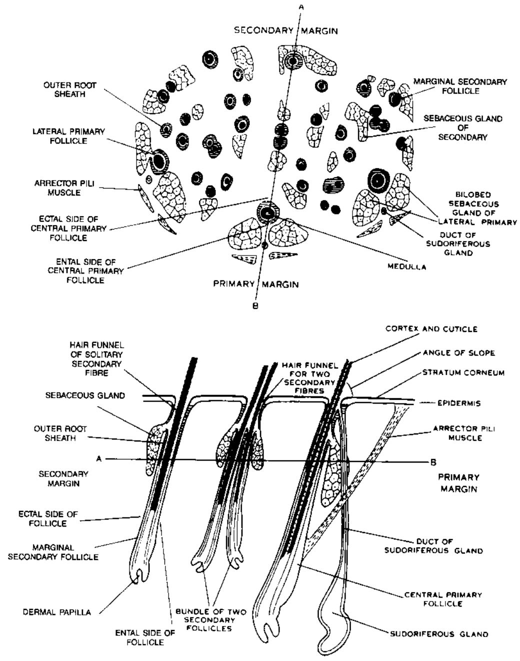
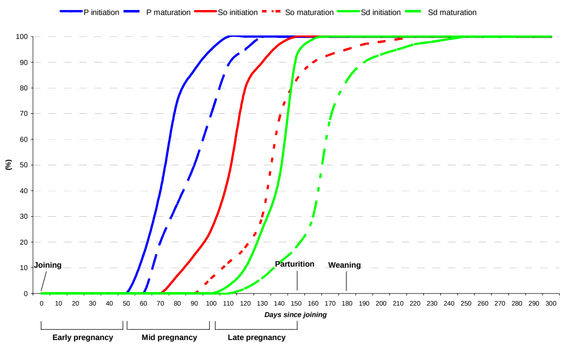
Appendix

Figure 1. The Merino follicle group as seen in (a) transverse and (b) longitudinal section.



Source: (Hardy and Lyne 1956)

Figure 2. The approximate timing of the initiation and maturation of primary, original and derived secondary follicles in sheep skin.



Source: The curves were drawn based on data from (Hardy and Lyne 1956; Fraser 1954; Ryder and Stephenson 1968; Short 1955a)

Table 1. The range of S/P ratio reported in the literature for various strains of Merino sheep

Strain	**S/P ratio**	
	Min	**Max**
Superfine		
Fine	**11:1**	**33:1**
Non-Peppin medium	**14:1**	**35:1**
Peppin medium	**12:1**	**46:1**
SA Strong	**8:1**	**28:1**

Source: (Carter 1955; Carter and Clarke 1957; Crook and Purvis 1997; Schinckel 1955a; Schinckel 1953)