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Feed affects the meat / wool tradeoff

Abstract

Parts of the Merino industry are concerned that selecting for high wool production may reduce reproduction and general fitness. This project examined fat reserves and energy metabolites in sheep that differed in EBV for clean fleece weight (CFW) and for coefficient of variation in fibre diameter (CVfd). The sheep were studied when fed below maintenance and in poor body condition, and again after re-feeding for 10 weeks. Sheep with a low CVfd had 50% more whole-body fat ($P < 0.05$) when they were underfed, but after re-feeding the difference was only 15% (NS). The EBV for CFW was not related to fatness, but interacted with EBV for CVfd to determine plasma IGF-1 concentration and glucose tolerance following challenge. We conclude that genetic selection for fleece characteristics can affect energy metabolism and reserves, which may account for the reported declines in reproductive performance. Importantly, the wool effects have greatest impact on sheep under nutritional challenge. Breeders selecting for wool should include reproduction or fatness traits in the breeding objective to enable the progeny to withstand the effects of nutritional challenge. Adoption of this advice will have a positive outcome for animal welfare.

Executive Summary

Why was the work done?

The efficiency of the Merino ewe flock is vital to the profitability of the Australian sheep meat industry (Pitchford, in press). Genetic correlations indicate that it should be straightforward to select for increases in both clean fleece weight (CFW) wool and total weight of lambs weaned, but Herselman *et al* (1998) in South Africa and Cloete *et al* (2002) in Australia both point out that this can only be achieved if liveweight increases concurrently. If liveweight is held constant, so that stocking rate can be maintained, there is a moderate negative genetic correlation between CFW and meat turnoff. Selection indices commonly used in the Merino industry still place some emphasis on increasing CFW, so it is important to determine the biological basis of the proposed antagonism between CFW and weaning rate.

The relationship between wool and reproduction appears to be mediated by fatness. There are significant genetic associations between measures of fatness and lamb growth rate (Lambe et al 2005) and many nutritional studies show that adequate fatness is essential for normal reproduction. Although CFW has a positive genetic correlation with liveweight, the correlation with fat depth is usually negative (Safari *et al* 2005). Adams *et al* (2005) reported that sheep with a high estimated breeding value (EBV) for CFW had less total body fat, and estimated that the difference could be sufficient to impair reproductive performance, if it had been established by nutritional manipulation.

Fatness also depends on nutritional history. To determine whether trade-offs between wool and reproduction are more severe when feed supply is limiting, we measured fatness in sheep that differed in EBV for CFW, in which poor and good body condition were established successively by offering different amounts of feed.

Genetic correlations indicate that fatness is affected by a range of wool characteristics apart from CFW, including the coefficient of variation in fibre diameter (CVfd), wool yield, and fibre curvature (Greeff *et al* 2005; Huisman and Brown 2005). In our previous study (Adams *et al* 2005), differences between groups in EBV for CFW were confounded with EBV for CVfd. Therefore, in the present study we compared groups that differed in either CFW or CVfd, to clarify which was the key driver of fatness.

What was achieved?

We showed that:

- Sheep with a low EBV for CVfd had higher levels of fatness when fed below maintenance. EBV for CFW did not have a significant effect on fatness.
- However, CFW interacted with EBV for CVfd for other measures of energy status, including subcutaneous fat depth, tolerance to glucose challenge, and plasma concentrations of IGF-1. This means that CFW affects the metabolic processes that probably drive the difference in fatness, and so may drive the rate of change in fatness.
- The proportional difference in fatness was greatest when sheep were on low nutrition. When they were in poor body condition, the low CVfd sheep had approximately twice as much fat (5.2 vs 2.7kg) as high CVfd sheep at the same liveweight. At high body condition, the absolute difference was similar (19.0 vs 16.5 kg), but this represented only 15% more fat, at similar liveweights and was not statistically significant.

- When fed *ad libitum* above maintenance on a high energy diet, high CFW sheep had a 7% higher feed intake, independent of liveweight.

When and how can industry benefit from the work?

This study has several important conclusions for the design breeding objectives for Merinos, including:

- Selection for wool characteristics may have significant effects on fatness and other indicators of the energy status of sheep. These effects are likely to affect reproductive efficiency, particularly if the sheep are in poor body condition. Therefore, traits such as the number of lambs weaned should be included in the breeding objective when sheep are selected for wool characteristics, especially where sale of surplus sheep and sale of meat animals makes a significant contribution to farm income.
- Where breeders are unable to select directly for reproduction rate, selection indices should aim to maintain fatness.
- Effects of wool characteristics on fitness (reproduction and survival) are likely to be most important when sheep are in low body condition. Therefore, these recommendations will find most ready acceptance in the highly seasonal annual pasture zones where reproducing sheep face annual 'droughts'. Implications for stocking rate need to be further developed.
- This work confirms previous suggestions that wool does not compete directly with meat for amino acids (otherwise CFW, not CVfd, would be the main driver of fatness). Mechanistically, there is no 'trade-off' *per se* between wool and muscle. Therefore, we may be able to achieve both withouit increasing liveweight, with a sound breeding objective that takes into account genetic relationships and relative economic values of all relevant traits.
- Because the effects of CFW and CVfd on some measures of energy status were not additive, it will be difficult to predict effects of wool selection on reproduction rate. Potential interactions with wool yield and curvature, which are also related to fatness, remain to be explored. Undefined genetic parameters may pose a problem in predicting genetic gain in lamb turnoff in flocks with active selection for wool characteristics.

Who can benefit from the results?

The outcomes from this research should be used by those Merino breeders and their clients who receive a significant proportion of their income from sale of both sheep and wool. Particular benefits will flow to:

- Merino breeders whose animals will be used in nutritionally challenging environments. This includes highly seasonal areas such as Western Australia and the cereal zone in most other States. It may also be relevant for growers where periodic droughts raise economic and welfare issues.
- MLA now has a strong biological basis to design and commission research to define nutritional environments where fitness characteristics are likely to be challenged.

Contents

1 Background

1.1 General introduction

Merino ewes form the mainstay of the Australian sheep meat industry, but we are still developing profitable breeding goals for Merino ewes to produce both meat and wool. Genetic correlations indicate that there is little or no conflict between improving production of wool and meat in breeding programs. However, many breeders struggle to get the right balance between fleece traits and reproduction and liveweight gain, due to apparent tradeoffs between wool and fitness traits that they observe at the phenotypic level.

The explanation for this attitude is becoming apparent. Although clean fleece weight (CFW) has a positive genetic correlation with liveweight, the correlation with fat depth is usually negative (Safari *et al.* 2005), and we have shown that sheep with a high EBV for CFW can have a substantially less total body fat, sufficient to potentially impair reproductive performance (Adams *et al.* 2005). Therefore, the metabolic effects of selection for high CFW need to be examined in terms of fatness, not muscle. Relative fatness may explain the linkage between high wool production and low reproduction.

There is a further ramification to this finding. Fat can be considered as a 'nutrient buffer' that may be used for fitness (van der Waaij 2004). Thus, high CFW sheep may have impaired fitness, at least when nutrient supply is sufficiently limited to reduce the effectiveness of the buffer. However, it is not known whether high CFW affects fatness under all nutritional states, or only when nutrient supply is low. Therefore, this experiment measured fatness in sheep with high and low EBV for CFW, when they were in low body condition, and then after re-feeding when in high body condition.

Greeff *et al* (2005) have indicated that fatness was not only related genetically to CFW (r_g ± s.e.m. = -0.29 ± 0.16), but was also related to several other fleece characteristics, including the coefficient of variation of fibre diameter (CVfd: r_g -0.41 ± 0.16) and yield (r_g -0.62 ± 0.15). In our previous experiment, CFW and CVfd were confounded, so it was not possible to be sure that the effects on fatness were due to CFW alone, or whether CVfd contributed. Therefore, the current experiment examined sheep with high and low EBVs for CFW, and for CVfd in a 2x2 design, to settle this question.

2 Project Objectives

2.1 Overall objective

The project aimed to provide MLA with advice on how sheep with high or low genetic value for CFW or CVfd respond in terms of body fat reserves when on a low or high nutritional plane. This information was needed to permit breeders to continue to select for wool characteristics in areas where nutritional shortfalls are common, without having deleterious effects on meat turnoff. The project also aimed to broaden previous results by examining effects of EBV for both CFW and CVfd, since these were confounded in a previous study.

2.2 Specific goals

2.2.1 Aim 1

To determine whether the EBV for CFW had a similar impact on the energy status (glucose and fat) of sheep when they were in low or in high nutritional status.

2.2.2 Aim 2

To determine extent to which previous observations on the effect of EBV for CFW on fat reserves were confounded by differences in the EBV for CVfd, and whether there is any interaction between EBVs for CVfd and CFW on measures of energy reserves.

3 Methodology

3.1 Sheep, management and measurements

3.1.1 Sheep

The sheep were sourced from the Katanning Merino resource flocks, derived from the Western Australian Department of Agriculture's Katanning Base Flock (Lewer *et al.* 1992). A total of 44 sheep was selected from the 550 measured ewe hoggets after shearing at 15 months of age. Fatness measurements and liveweight taken at that time were used, together with pedigree information, to calculate EBVs. The sheep were used in a 2x2 factorial design with EBV for CFW and CVfd as factors, as shown in Table 1. Sheep were stratified as high (H) or low (L) CFW per unit liveweight, and on high (H) or low (L) CVfd within these groups. Animals were selected to have similar mean EBV for liveweight in each cell to simplify comparisons of body composition, although the L CVfd group tended to have a greater EBV for liveweight (P = 0.06).

Table 1 Mean (± s.e.m.) estimated breeding value (EBV) for clean fleece weight (CFW), coefficient of variation in fibre diameter (CVfd), subcutaneous fat depth (Fat) and liveweight (LWT) in the four groups of sheep

Group CFW/CVfd	N	EBV_CFW (kg)	EBV_CVfd (%)	EBV_Fat (mm)	EBV_LWT (kg)
HH*	10	0.29 ± 0.02	2.5 ± 0.2	-0.12 ± 0.1	0.7 ± 1.1
HL	11	0.35 ± 0.02	-1.6 ± 0.2	0.04 ± 0.1	2.7 ± 1.1
LH	12	-0.21 ± 0.02	1.7 ± 0.2	-0.06 ± 0.09	1.7 ± 1.0
LL	11	-0.26 ± 0.02	-3.0 ± 0.2	0.75 ± 0.1	3.9 ± 1.1

*H = high, L = low

Overall genetic correlations within this flock are similar to those reported for the Australian flock by Huisman and Brown (2005). Among the sheep selected, the groups differed significantly in EBV for subcutaneous fat depth, which had been measured by ultrasound at 15 months (Table 1). This occurred mostly because of an interaction between CFW and CVfd (P = 0.002), such that the LL group had a higher EBV for fat depth than all of the other groups (Table 1). As a result of this interaction, fat depth was lower in sheep with high CFW (P < 0.001),and with a high CVfd (P < 0.001). The groups did not differ significantly in EBV for eye-muscle depth (data not shown).

Overall, the mean EBV for CFW was similar in the two CVfd groups, but there was an interaction ($P < 0.01$) such that low CVfd was associated with a higher CFW in the high CFW group, but a lower CFW in the low CFW group (Table 1). The EBV for CVfd was higher in the high CFW group ($P < 0.001$), but the effect was relatively small (Table 1) and there was no interaction between CFW and CVfd. The groups did not differ significantly in EBV for fibre diameter (data not shown).

3.1.2 Animal management

The sheep were managed in the paddock under normal husbandry at Katanning during early autumn to obtain low body condition, before transport to the CSIRO Floreat animal house. The sheep were drenched with a broad spectrum anthelmintic (Triton: Merial Aust., Parramatta NSW 2150) and offered milled oaten hay + 10% lupin seed for 10 days before the experiment started. On Day 0, sheep were offered this feed at 0.8x energy maintenance (M) as calculated by Grazfeed (Horizon Technologies Ltd, Armidale NSW), and this feeding regime continued until Day 42.

On Day 43 the sheep were offered a high energy ration containing 11.3 MJ/kg dry matter and 13% crude protein (20% lupins, 25% barley, 48% oaten hay with an *in vitro* digestibility of 61.7% and crude protein of 6.9%, 5% molasses and 2% Siromin mineral mix). The amount of feed offered was increased daily in 100g increments, and refusals measured to determine voluntary feed intake. Sudden declines in feed intake in some sheep were managed by reducing feed offered, followed by gradual restoration. On Day 86 all sheep were fed at 1.2M, which was maintained so that their response to glucose infusion could be studied without confounding effects of differences in feed intake. Feeding *ad lib* was resumed on Day 101 and continued until the end of the experiment.

Sheep were weighed weekly before feeding throughout the experiment.

3.1.3 Measurements

Body composition was estimated by dilution of deuterated water on Day 33 and Day 148, following the procedure of Searle (1970), and the concentration of deuterium measured in a GC/MS after exchange with labelled acetone as described by Yang *et al* (1998). Fatness was measured again using a Norland XR-46 DEXA (dual energy X-ray absorptiometer) on Day 170. Eye-muscle and fat depth were measured by a commercial operator using ultrasound on Day 184.

Blood samples were collected weekly and the concentration of insulin-like growth factor-1 (IGF-1) was measured by our established radio-immunoassay (Adams et al 1996).

To measure the capacity to respond to glucose, a subset of 4 sheep from each group (total 16 sheep) were fitted with bilateral jugular catheters and infused intravenously with a solution of glucose in saline on Day 29 and again on Day 98. The same sheep were used on each occasion. The sheep received a priming dose of 110 mmol glucose followed by a continuous infusion of 2 mmol/h in saline for 3 hours. Plasma samples were taken from the opposite catheter each 30 min, and the concentration of glucose was measured by autoanalyser.

3.1.4 Statistical analysis

Data were analysed statistically with the package Systat (SPSS Inc., Chicago IL, USA) using analysis of variance and general linear models. Liveweight gain was estimated from the regression of liveweight on body weight in two separate periods, separated by feeding at 1.2M on Days 86 to

101. Period 1 included liveweight measurements between Day 48 and Day 87, and Period 2 included liveweights between Day 101 and Day 145. Mean feed intakes were calculated for each week and analysed by repeated measures analysis of variance over these same periods of *ad lib* feeding (Days 47 to 86 and Days 101 to 147). The calculated intercept for liveweight in each period was used as a covariate in feed intake analysis, to account for the effects of liveweight (but not liveweight gain) on feed intake.

4 Results and Discussion

4.1 Liveweight gain

The mean liveweights were similar in the 4 groups, but regression analysis indicated that high CFW sheep gained more liveweight in Period 1 than low CFW sheep (0.29 *vs* 0.24 ± 0.01 kg/day, P = 0.02). This difference was not apparent in Period 2 (high vs low CFW being 0.21 *vs* 0.20 ± 0.01 kg/day, NS), although the greater gain in Period 1 resulted in the intercept tending to be higher in the high CFW sheep in Period 2 (52.4 *vs* 50.8 ± 1.0kg, P = 0.07). There were no significant effects of CVfd on liveweight or liveweight gain. Average values for liveweight at the beginning and end of the experiment are presented in Tables 2a and 2b.

4.2 Feed intake

All sheep increased voluntary feed intake dramatically once restriction was lifted (Figure 1). This increase continued longer in the high CFW sheep. As a result, in Period 1 the high CFW sheep ate more (P < 0.05) and had a different pattern of intake over time (P < 0.01), as illustrated in Figure 1. Analysis using the liveweight or fatness as covariates did not change these conclusions, indicating that the higher intake did not result from differences in metabolic mass. However, the high CFW sheep gained more liveweight over this period.

Feed intake in Period 2 was approximately 7% higher in the high CFW group, even when liveweight was accounted for (P < 0.05: Figure 1). Thus, the CFW effect was not due to the slightly higher liveweight in the high CFW group. The gain in fatness over the experimental period was similar in the high and low CFW groups (see Tables 2a and 2b below), indicating that the additional feed intake did not result in additional gain in fatness. It is concluded that, as reported previously (Adams *et al* 2005), a high EBV for CFW is associated with a slightly higher voluntary feed intake.

The higher feed intake in the high CFW sheep therefore indicates a higher metabolic rate. This could result if high CFW is associated with higher whole-body protein turnover, as suggested by Adams *et al* (2004). Protein turnover makes up about one quarter of basal energy expenditure in Merinos, so if the entire difference was due to increased protein turnover, this would require turnover to be 25% greater in the high CFW group. This compares favourably with a 19% greater appearance rate of endogenous phenylalanine in high compared with low CFW ewes within a flock reported by Adams *et al* (2004).

CVfd was not related to feed intake in either period, even though it was associated with differences in body fatness.

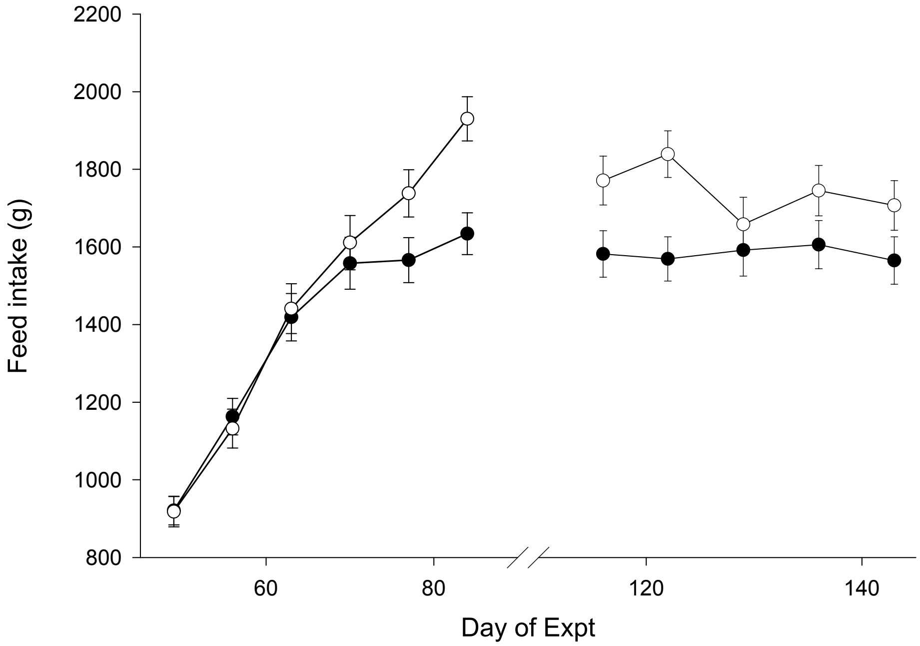

Figure 1. Mean and s.e.m. voluntary feed intake in high CFW (○) and low CFW (●) sheep during the two periods of *ad lib* feeding.

4.3 Fatness

During the period when sheep were in low body condition, measurement of body composition by deuterated water on Day 33 indicated that the low CVfd sheep tended to have a greater empty liveweight (P = 0.06, Table 2a). The low CVfd sheep had greater fat reserves (6.4 *vs* 3.4 kg, Table 2a, P < 0.05), and a greater proportion of fat in the body (P = 0.05, Table 2a) compared with high CVfd sheep. There was no interaction between CFW and CVfd for any body component.

Table 2a. Body composition in low body condition at Day 33 (mean ± s.e.m.)

Group	Mean empty LWT (kg)	Fat (kg)	Lean (kg)	Proportion of fat (%)
H/H	40.6 ± 1.4	4.2 ± 1.0	36.0 ± 2.5	10.7 ± 2.5
H/L	44.2 ± 1.8	6.4 ± 1.3	37.4 ± 1.1	14.0 ± 2.8
L/H	41.1 ± 1.4	2.6 ± 1.1	38.3 ± 1.9	6.6 ± 2.9
L/L	42.6 ± 1.4	6.4 ± 1.2	35.9 ± 1.4	15.1 ± 2.7

It is likely that the current feeding level did not play a great role in these results. The low body condition was established mostly in the paddock before the sheep entered the animal house, and there was little additional loss of liveweight during the 33 days that the sheep were fed at 0.8xM. Therefore, these results may be reasonably representative of hogget sheep run in the paddock in Western Australia during autumn, unless they receive strong supplementary feeding.

At the end of the experiment, fatness measured by DEXA on Day 170 indicated similar amounts of fatness in all 4 fleece groups, although it tended to be higher ($P = 0.08$) in sheep with a low CVfd (Table 2b). Note, these values do not represent the total fat in the body, because parts of the body including the brain were omitted from the DEXA scan. The low CVfd sheep tended to have more fat ($P = 0.14$) when fat mass was expressed as a proportion of liveweight (% Fat, Table 2b).
Ultrasound measures on Day 184 indicated no significant effect of either CFW or CVfd on either fat or muscle depth (Table 2b). Although the L/L group appeared to have a slightly greater fat depth than the other groups, the interaction did not achieve statistical significance ($P = 0.16$: Table 2b).

Table 2b. Body composition at the end of experiment (mean ± s.e.m.)

Group	Mean livewt Day 145 (kg)	Fat by DEXA (kg)	fat by DEXA (%)	Fat depth C site ultrasound (mm)	Muscle depth C site ultrasound (mm)
H/H	61.6 ± 1.9	16.2 ± 1.5	28.2 ± 2.3	5.7 ± 0.5	27.7 ± 0.8
H/L	64.7 ± 1.8	19.3 ± 1.5	31.8 ± 2.3	5.4 ± 0.5	27.4 ± 0.7
L/H	61.0 ± 1.7	16.7 ± 1.4	29.8 ± 2.0	5.4 ± 0.4	26.4 ± 0.7
L/L	60.8 ± 1.8	18.7 ± 1.5	33.1 ± 2.2	6.5 ± 0.5	26.8 ± 0.7

Previously Adams *et al* (2005) examined sheep that differed in EBV for fibre diameter and CFW, and reported that differences in fatness were associated with EBV for CFW. However in that study the CFW groups also differed in CVfd, because a high CVfd is associated genetically with high CFW (Cloete *et al* 1997). The present results indicate that in fact, the differences in that study were more likely due to confounding differences in CVfd.

A previous study reported relative changes in body composition in sheep that differed genetically in staple strength, and so in CVfd, but did not differ significantly in EBV for CFW. During a period of liveweight loss while grazing dry autumn pastures, the high staple strength (low CVfd) sheep maintained fat reserves better, losing relatively more lean tissue (Adams *et al* 1997). This is consistent with the greater capacity of low CVfd sheep to maintain fat reserves under nutritional stress in the present study. Further work is required to determine how the quality of the feed (digestibility and proportion of protein) interacts with genotype in determining relative body composition.

The depth of subcutaneous fat is normally measured at the time when fatness is greatest to minimize measurement error in Merinos, which normally have low fatness. However, Lambe *et al* (2004) showed that within year correlations of EBV for fat depth are surprisingly low. Furthermore, subcutaneous fat depth is not well related to total body fat (Table 1, Table 2b). Therefore, there would be industry benefit in developing better indicators of total body fat at times when the animals are under nutritional stress.

4.4 Plasma metabolites

4.4.1 Glucose

Intravenous infusion of glucose into the sheep when they were in a low nutritional state (Day 29) resulted in a substantial increase in plasma glucose concentration ($P < 0.001$; Figure 2). The pattern of plasma glucose concentrations over time differed between the high and low CVfd groups ($P < 0.01$).

This study is the equivalent of a 'glucose tolerance test' in human patients. The increase in plasma glucose concentrations indicates the failure of insulin to maintain homeostasis. These results therefore indicate that the sheep were relatively insensitive to insulin at this time, but that the low CVfd sheep were slightly more sensitive to insulin than high CVfd sheep. This is consistent with their higher fat reserves at this time

On Day 98 (55 days after re-feeding commenced) basal plasma glucose concentrations were higher than at Day 29 ($P < 0.01$) and the plasma glucose response to infusion was slight ($P < 0.05$). As shown in Figure 2, an increase in plasma glucose after infusion was observed only the L/H group. Comparison of the two infusions indicated a trend for the interaction between CFW and CVfd for mean glucose concentration to be significant across time ($P = 0.08$). As shown in Figure 2, this resulted primarily from the greater plasma glucose concentration in the L/H group at the second infusion, compared with the first.

The results indicate that the L/H group maintained a relative insensitivity to insulin during early re-feeding. Interestingly, this group also had the lowest amount of fat when they were in low body condition at Day 33 (Table 2a).

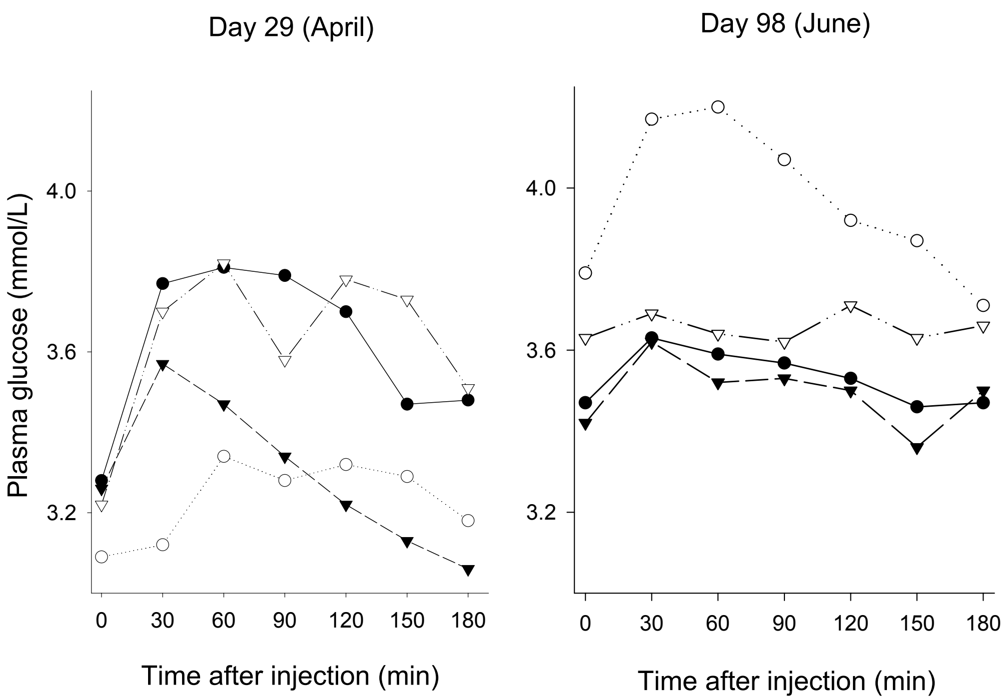

Figure 2. Plasma glucose response to glucose infusion before and after re-feeding commenced on Day 43. The four CFW / CVfd groups are: H/H (◊), H/L (▼), L/H (○) and L/L (●).

Measurements of plasma insulin concentration are not yet complete, but preliminary analyses indicate that on Day 29 the mean concentration of insulin (1.04 µg/L) did not differ between groups. In contrast, the previous study (Adams *et al* 2006) found higher plasma insulin in the high CFW / high CVfd group. However, no difference in plasma insulin or in glucose concentration was observed between sheep that differed in EBV for staple strength, and so for CVfd (Adams *et al* 2000). This is consistent with the conclusion suggested by Figure 2: that effects on glucose metabolism depend largely on interactions between the EBVs for CFW and CVfd.

4.4.2 IGF-1

Plasma concentrations of IGF-1 were low on Day 27 in sheep fed below maintenance (Table 3), and there was an interaction between CFW and CVfd ($P < 0.05$), due to high values in the L/L group (Figure 3). Re-feeding commenced on Day 43, and by Day 98 the concentration of IGF-1 was increased ($P < 0.001$). Values for the L/L group were again greater, although the difference was less marked (Figure 3).

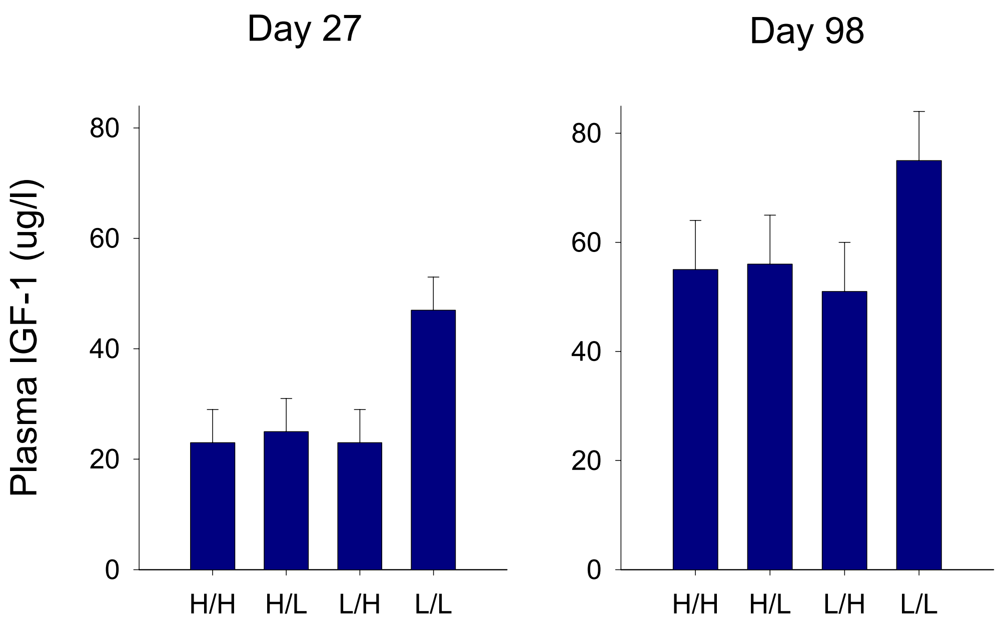

Figure 3. Mean (s.e.m. error bars) concentrations of IGF-1 (µg/L) in plasma of sheep from the four groups before (day 27) and after (Day 98) re-feeding on Day 43.

These results are consistent with previous studies. Adams *et al* (2000) examined sheep with high and low EBVs for staple strength, but similar CFW, and found that high staple strength sheep (with low CVfd) had higher plasma IGF-1. High plasma IGF-1 was also observed in sheep with low EBVs for CVfd and CFW (Adams *et al* 2006). The present study extends these observations by showing that the effect of CVfd on IGF-1 can be modulated by the EBV for CFW (Figure 3).

A high plasma concentrations of IGF-1 has been shown to be associated with increased fatness in other species (eg, Bunter *et al* 2005), and it is noteworthy that the L/L group, which had the greatest EBV for subcutaneous fatness (Table 1) also had the highest plasma IGF-1. These results indicate that plasma IGF-1 might be used as an indicator of fatness in sheep, particularly when they are in lean body condition.

4.5 General discussion

Taken together, two further important points arise. Firstly, interactions between CFW and CVfd were important for fatness and for metabolic indicators. Thus, the L/L group stood out as having high subcutaneous fat and high plasma IGF-1, while the L/H group had the greatest glucose intolerance (Figure 2) and the lowest total body fatness (Table 2a). In other words, the main effects alone do not provide an accurate basis for predicting the effects of selecting for fleece characteristics on energy metabolism.

Secondly, the results are consistent with hypothesis that metabolic control differs among fat depots, as has been described in humans (Miyazaki *et al* 2002). Thus, patterns of difference in subcutaneous fat reflected differences in plasma IGF-1 (Table 1, Figure 3) while differences in total body fat in sheep in poor condition (Table 2) were most closely paralleled by differences in glucose tolerance (Figure 2). There is further evidence that the functional significance of fatness for reproduction depends on the depot in which it is located. Lambe *et al* (2005) suggest that, if liveweight is constant, low internal fat at lambing and low carcass fat at weaning have the strongest genetic associations with lamb growth rate. Therefore, it will be important to determine the most appropriate measure of fatness, and the best relationship between this measure and the level of fatness at the appropriate time in the reproductive cycle, before confident recommendations can be made.

5 Success in Achieving Objectives

The study achieved both its specific goals. Firstly, we proved that differences between sheep in EBV for fleece characteristics have their greatest effect on fatness when sheep are in poor body condition. Because fatness influences reproduction and capacity to withstand prolonged low feed supplies, this result indicates that breeding goals for Merinos should consider fitness goals such as reproduction and survival, especially if it is anticipated that the sheep will encounter nutritional challenge. These results confirm and extend previous observations, and so are likely to have general applicability.

Secondly, the study found that EBV for CVfd was more closely related to fat reserves and energy metabolites than was EBV for CFW. Previous studies had not distinguished between the effects of CFW and CVfd. Even more importantly, we found interactions between CFW and CVfd, indicating that neither characteristic can be considered in isolation from the other. Huisman and Brown (2005) and Greeff *et al* (2005) observed that other wool characteristics including yield and fibre curvature are also related to fatness. Therefore, attempts to manipulate fatness (and presumably fitness) by selecting for specific fleece characteristics need to take into account all significant relationships, including interactions among fleece characteristics.

6 Impact on Meat and Livestock Industry – now and in five years time

6.1 Immediate impact

This study has produced two messages that MLA can use to help breeders to improve meat turnoff with less impact on wool productivity:

6.1.1 Do not penalise wool to improve meat production

There is no simple trade-off between meat and wool, so Merino breeders can to continue to improve wool productivity.

Many Merino breeders have reduced the emphasis on wool in their breeding objectives, often assuming that this will enhance reproduction and fitness. However, the present results confirm that this is a very ineffectual approach to improving meat turnoff. We showed previously that conflicts between meat and wool do not depend on competition for amino acids, and the present work provides further evidence that effects of wool genotype on fatness, and so on meat turnoff, are not exerted by CFW alone. We found that CFW and CVfd interact to affect fatness, glucose sensitivity, and IGF-1. Preliminary studies suggest that interactions between CFW and CVfd for fat depth also occur in other populations, and Greeff *et al* (2005) indicate that wool yield and fibre curvature also affect fatness. Therefore, selecting for specific fleece characteristics is a very inefficient way to improve meat turnoff. Breeders should be encouraged to select directly for reproductive efficiency.

6.1.2 Breed for increased fatness in some environments

Breeders who are unable to select ewes directly for reproduction rate should be able to maintain reproductive turnoff in high wool producing Merinos by maintaining fatness. This can be achieved through better nutrition, but in poorer environments genetic selection to increase fatness in Merino dams should also be effective in maintaining fitness.

Some growers have been selecting Merinos for decreased fatness, to produce leaner lamb. Simple desk-top studies comparing benefits from reducing fatness to enable Merino and Merino-cross lambs to meet market targets *vs* the potential increases in lamb turnoff and ewe resilience are needed to enable more informed recommendations to be made. The outcome would assist breeders to determine appropriate targets for fatness in their Merinos.

6.2 Anticipated impact in 5 years time

This work should change the way that scientists and growers think about the impact of selection for wool characteristics on the robustness of their sheep. Studies show that the uptake of quantitative genetics by Merino breeders is inhibited by their concern over biological tradeoffs between wool production and the sheep's capacity to withstand harsh environments (Kaine and Niall 2001). The present work offers a way to account for resilience within a framework of quantitative genetics, and so should help overcome the gap between woolgrowers and quantitative genetics. Greater acceptance of scientific methods could have a beneficial impact on the industry and its politics.

More specific benefits that might be expected include:

6.2.1 Better measures of 'environment'

These results suggest that body fat reserves are an important metabolic indicator of nutritional history, and so can be used as a key descriptor of environment. Body condition score is a poor measure of fat reserves, but it too could be used to indicate nutritional history. Realistic assessments of 'environment' from a measure on the sheep allow more targeted breeding objectives.

6.2.2 Improved animal welfare

Industry is under ever-greater scrutiny on welfare. These results give an opportunity to take a proactive stance on the selection of sheep that can withstand low feed supplies. This should enhance the capacity of ewes to keep lambs alive during periods of feed deficiency and drought.

6.2.3 Need for genetic marker

This report highlights the need for better markers of nutritional reserves, particularly fatness. Subcutaneous fat depth is often difficult to measure in Merinos. The beef industry has an active program studying DNA markers for fatness, marbling, etc. Hopefully the present study will promote interest by the sheep industry in the potential value of such a marker, and follow developments by beef researchers.

7 Conclusions and Recommendations

7.1 Conclusions

1. Genetic selection for wool characteristics can affect the body composition and energy metabolism of Merinos
2. These effects are most marked when sheep are in low body condition. High CVfd sheep had about 50% less fat in their bodies when they were at low body weight, but only 15% less fat after re-feeding, compared with low CVfd sheep.
3. Effects of wool characteristics on metabolism are not simply additive. Interactions between CVfd and CFW were observed for plasma IGF-1 concentrations, EBV for subcutaneous fat depth, and responsiveness to glucose challenge.
4. The previously observed difference between high and low CFW sheep in total body fat was probably due to associated differences between the groups in CVfd.

7.2 Recommendations

7.2.1 Industry

Many Merino breeders would benefit from an MLA / SGA awareness program to improve the choice of breeding goals. Messages include:

1. Breeders can continue to select for increased fleece weight, because there is no simple trade-off between wool and meat.
2. Merino breeders should include reproduction traits in their breeding objective, unless the sheep will be used solely for wool production. This applies particularly if the sheep will be subject to nutritional challenge.
3. Breeders who cannot select directly for reproduction may maintain fitness and reproduction by ensuring a positive outcome for fatness from their selection index.

7.2.2 Research

Further research would enhance the capacity of industry to apply the findings from this project. The following outcomes are needed:

1. Relationship between EBV for fatness and reproductive success. This should be possible using data already available, provided that it provides sufficiently accurate indications of ewe conception rate.
2. Robust indicators of the nutritional environment. The current work suggests fatness is a good potential indicator. However, it is not clear whether this applies similarly to perennial pastures (where protein / energy ratio is usually adequate and energy is limited largely by stocking rate) and to annual pastures (where protein concentration differs dramatically through the year). At present, it is not known whether the results have greatest applicability to breeders in the cereal zone or in the high rainfall zone. Resolution of this question is essential.

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